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Social Behavior and Cooperative Breeding of Kalij Pheasants (*Lophura leucomelanos*) in Hawai'i

A Dissertation submitted in partial satisfaction
of the requirements for the degree of

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in

Evolution, Ecology and Organismal Biology

by

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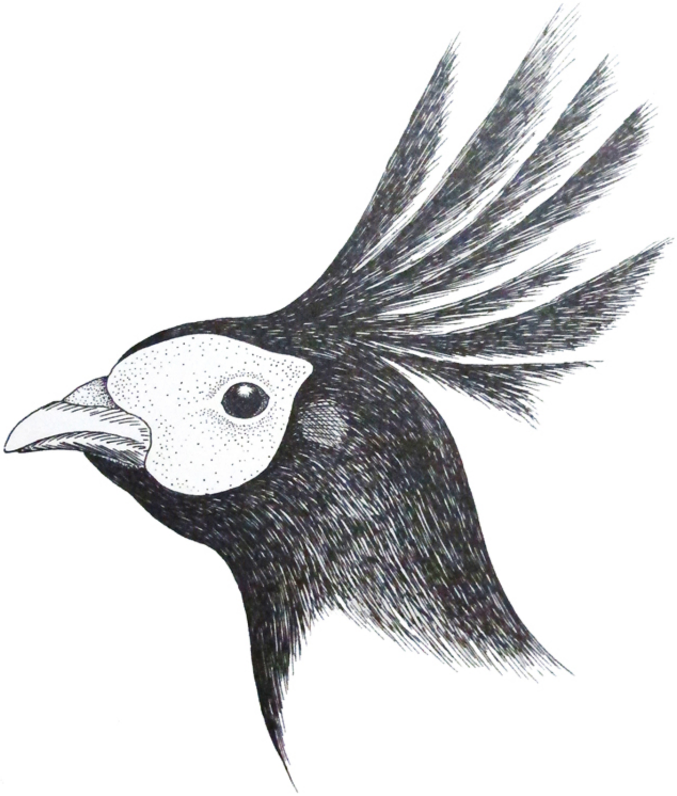

Kalij Pheasant illustration by Lijin Zeng

Following figure 34 in book "The Pheasants of The World" by Johnsgard 1999

ABSTRACT OF THE DISSERTATION

Social Behavior and Cooperative Breeding of Kalij Pheasants (*Lophura leucomelanos*) in Hawai'i

by

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Cooperative breeding is an evolutionarily curious behavior, because helpers appeared to altruistically forgo opportunity for their own reproduction. In a population of Kalij Pheasants *Lophura leucomelanos* introduced to Hawai'i, we recorded cooperative breeding behaviors including caring for chicks, defending against conspecific intruders, and vigilance against predators. While cooperative breeding mostly occurs in altricial species, in which offspring need substantial parental care to survive, such behavior in the precocial Kalij Pheasants with relatively independent offspring provides an excellent opportunity to examine cooperative breeding and its influencing factors without the constraint of intense offspring needs. In our study population, Kalij pheasants formed stable social groups that usually contained one female and one to six males, and larger groups maintained larger year-round home ranges in general. One male was dominant among others within a social group, and age was the only factor found to determine dominance, indicating helpers can possibly stay in social groups and queue for dominance. Because high density was observed, we hypothesized that breeding habitat may be saturated, and that subordinate males cannot establish independent breeding habitat and subsequently remain in social groups. The removal of about one third of social groups resulted in a significant decrease in number and proportion of multiple male groups, and suggested that habitat saturation contributed to cooperative breeding in this population. To examine if helpers gained genetic benefits, we used 12 autosomal microsatellites and applied relatedness and parentage analyses to 88 adult and 82 offspring samples. On one hand, we found 34.4% subordinate males were related to the dominant male of the social group, indicating some helpers can gain inclusive fitness by helping kin. On the other hand, subordinate males fathered 16.5% of offspring sampled, suggesting that helpers can gain direct fitness be participate in reproduction. These results helped to understand the maintenance of cooperative breeding in this population; however, the causes for cooperative breeding can be complex in reality. In addition to examined factors, group-living benefits and life history traits may also have played a role in cooperative breeding in Kalij Pheasants.

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General Introduction

General Background

Although Alexander Skutch first brought up the existence of the seemingly altruistic cooperative breeding behavior and different forms of helpers-at-the-nest in birds in 1935 (Skutch 1935), the phenomenon has been intensively studied only in the last four decades. Cooperative breeding behavior occurs in reproductive groups when one or more group members voluntarily provide help to genetically related or unrelated individuals in finding a mate (e.g., coordinated displays in wild turkeys *Meleagris gallopavo*, Krakauer 2005), in acquiring and defending a territory (e.g., Galapagos mockingbird *Nesomimus parvulus*, Curry and Grant 1990), or in caring for offspring (e.g., Red-cockaded woodpecker *Picoides borealis*, Walters et al. 1988). It was specifically defined as "a reproductive system in which one or more members of a social group provide care to young that are not their own offspring" by Stacey and Koenig (1990), where the sexually mature aid-givers may be "genuine helpers" that do not breed (e.g., last year's offspring of the Australian bell miner *Manorina melanophrys* Latham, Clarke 1984), or co-breeders that share reproduction with other group members of the same sex (e.g., wild turkeys, Krakauer 2005). The helping behavior usually increases the offspring survivorship of the breeding group, and the breeders being helped usually either gain increased reproductive success in that breeding season or increased accumulative inclusive fitness over a lifetime.

Cooperative breeding is a behavior of particular evolutionary significance because helpers appear to forgo the opportunity to reproduce for themselves, at least temporarily or partially. This seemingly altruistic behavior is intuitively evolutionarily unstable; however, helpers can gain direct and indirect benefits such as mating with breeders (Koenig 1981), helping kin (Hamilton 1964; Maynard Smith 1964; Woolfenden and Fitzpatrick 1984), or becoming a breeder in the group later (Kokko and Johnstone 1999).

Cooperative breeding has most often been found and studied in altricial species, in which the helpless hatchlings need extensive care and can receive strong benefits from helpers (Krebs and Davies 1993). By contrast, cooperative breeding in precocial species is very rare (Langen 2000), and the benefits of cooperation, given that offspring require less direct care, remain poorly understood. Cooperative breeding in precocial species has been rarely studied, in part because independent hatchlings require less direct care, which makes cooperative breeding in precocial species seem insignificant. However, because the intensive offspring needs - one of the generally recognized original impetuses for such behavior - are missing, cooperative breeding in precocial species provides an exceptional opportunity to disentangle the influences of other contributing factors that have shaped the cost-benefit relationship related with such seemingly altruistic behavior beyond the influence of intensive offspring needs. Such study is important for a synthetic understanding of cooperative breeding behavior and its evolutionary maintenance in general.

Factors known to influence the evolution of cooperative breeding include ecological constraints, reproductive share, kinship patterns, demographic characters, and life history traits. In addition, expanding the study of cooperative breeding from restricted to altricial species to also include precocial species can provide greater variation in interspecific comparative analyses parameters, such as physiological and life history characteristics, and subsequently increase the power of such analyses that can reveal significant findings across species. Lastly, the existence of cooperative breeding in precocial species makes a strong case for the influence of such factors on cooperative breeding in general. If offspring demand for intense parental care is a critical factor promoting cooperative breeding, then the presence of cooperative breeding in precocial species with reduced parental care highlights the influence of other ecological factors in shaping this behavior. Therefore, the study of precocial species would fill a major gap in our understanding of the factors influencing cooperative breeding.

Two major questions for understanding the evolution of cooperative breeding have been identified during the past four decades: (1) "why do helpers stay" and (2) "why do they help" (Stacey and Koenig 1990). For the first question, ecological constraints hypothesis (Emlen 1982b, a, 1984), and benefits of philopatry hypothesis (Stacey and Ligon 1987, 1991) have been proposed and tested. The ecological constraints hypothesis suggests that ecological limitations can prevent some individuals from breeding independently, therefore breeding cooperatively makes the best of a bad situation; the benefits of philopatry hypothesis suggests nonbreeding helpers can gain benefits from remaining in the cooperative group, such as when territory quality of the group is superior to surrounding areas. Among ecological constraints, habitat saturation (Selander 1964; Brown 1987) is widely found in cooperative species and well supported by empirical studies (e.g., Komdeur 1992; Stacey 1979); mate limitation (e.g., Fessl et al. 1996; Pruett-Jones and Lewis 1990) can also be important and is commonly considered. For the latter question, the hypotheses of kin selection (Hamilton 1964; Maynard Smith 1964), direct (Trivers 1971) and indirect reciprocity (Nowak and Sigmund 1998), direct fitness gains (Reyer 1984), group selection (Maynard Smith 1964)) and proximity to begging young (Craig and Jamieson 1990) have been proposed, and each of them is still under debate.

Field examination on influencing factors and manipulation experiments can provide insights into how ecological constraints influence cooperative breeding. However, genetic investigation of relationships and reproductive share among individuals in the population is needed for characterizing the true mating system and inferring the breeding strategies of cooperative breeders. In fact, genetic analyses have revolutionized our understanding in the past few decades and have now become a standard for estimating parentage as well as other kinship relations between individuals (Sinervo and Zamudio 2001).

Study System

Avian species afford good opportunities to study cooperative breeding, and studies focusing on birds have played a preeminent role in this area (Hatchwell and Komdeur 2000). Advantages of using birds to study cooperative breeding include the fact that this taxon is diverse, with representatives in almost all types of environments, which facilitates a comparative approach to look at relationships between behaviors and the various factors influencing them (Bennett and Owens 2002). In addition, birds can be permanently marked, and the behavior and relationship among individuals can be easily observed and tracked across multiple years. Moreover, birds comprise the only class of vertebrates in which most species exhibit social monogamy and well-developed male parental care, and thus may be predisposed to the evolution of cooperative breeding (Hatchwell and Komdeur 2000).

Pheasants (Galliformes:Phasianidae), being precocial species, provide a new angle to the study of cooperative breeding. First, cooperative breeding in precocial species appears less likely than in altricial species since their independent young demand less parental care, and it has not been well-studied in precocial birds such as pheasants. Indeed, cooperative breeding in pheasants has been reported only twice in current literature (Lu and Zheng 2005; Xu et al. 2011). However, such studies are important for a synthetic understanding of such behavior. Second, sexual dimorphism and showy plumage among males in pheasants suggests strong sexual selection on males, making it appear less likely for males to breed cooperatively. When cooperative breeding does occur among pheasants, it strongly suggests that ecological constraints or other factors are influencing such behavior. In addition, pheasants as a family exhibit large variation in breeding systems, but the reason why these physiologically similar species would demonstrate different mating systems from dominant polygyny to monogamy and polyandry is not clear. Among pheasants, species with high within-species mating system variation are likely to prove advantageous subjects of study, because the more plastic the system is, the more likely it flexibly reacts to environmental conditions, which may show a stronger relationship between helping behavior and environment factors.

On the island of Hawai'i, I recorded cooperative behavior of Kalij Pheasants *Lophura leucomelanos,* a precocial species. Thane Pratt first observed the cooperative behaviors among males in social groups with multiple males and one female. Available literature on limited ecological observation of Kalij Pheasants in their native habitat in the Himalayas (Ali and Ripley 1969; Barnes 1981; Delacour 1989; Iqbal 1992; Johnsgard 1999), and

Hawai'i (Lewin and Lewin 1984) suggests that the mating system of the Kalij pheasant may be monogamous or polygynous depending on the circumstances, reducing the likelihood of cooperative breeding among males. The possibly recently arisen novel adaptation of cooperative breeding behavior in a species introduced to a new environment provides a unique system to study the ecology and influencing factors that have shaped the evolution and maintenance of such behavior.

The basic ecology and behavior of Kalij Pheasants had not been intensively studied previously. Nine morphologically distinct and geographically separated subspecies that comprise the species live mainly on the west side of the Himalayas across various habitat types from mountainous forests to lowland cultivated lands and forests (Barnes 1981). The subspecies can interbreed, and sometimes interbreed with subspecies of the closely related Silver pheasant *Lophura nycthemera* (Phillips 1921; Hennache et al. 2003). The Hawai'ian population is a cross of two subspecies: the white-crested Kalij (*L. l. hamiltoni*) and dark-crested Kalij (*L. l. leucomelanos*), and individual phenotypes are quite variable (T. K. Pratt, unpubl. data). The Hawai'ian population was introduced onto the Pu'u Wa'awa'a Ranch in 1962, established with 67 game birds collected from Michigan and Texas game farms (Lewin and Lewin 1984). After that, the population flourished and became a legal game species in 1977. It is widely distributed in various types of forests from sea level to 2450m elev., with a concentration between 450 and 2150m on the island

(Lewin and Lewin 1984). The current island-wide population is estimated to be over 100,000 (T. K. Pratt, unpubl. data). It is suspected to be a reservoir of avian disease, especially malaria, and possibly impacts native fauna and flora via its food preferences, or indirectly by seed dissemination of exotic plant pests (Lewin and Lewin 1984). However, it is not currently considered a major threat to the conservation of native Hawai'ian forest birds.

The study site is at Kipuka Puaulu (a.k.a. Bird Park) on the southeastern flank of Mauna Loa volcano on the island of Hawai'i, USA, within Hawai'i Volcanoes National Park. A kipuka is an area of forested hills isolated by historic lava flows, providing a spatially patchy distribution of the old-growth forest resource suitable to the forest-dwelling Kalij Pheasants. Sparsely vegetated shrub lands in between kipukas and other forests are less fit for foraging or roosting, and incur potentially higher predation risk for the Kalij. Consequently, the Kalij population within Kipuka Puaulu is relatively stable and semi-isolated. Indeed, individuals banded in Kipuka Puaulu were found in neighboring Kipukas and forests only for few cases (T. K. Pratt, unpubl. data), which suggest that landscape structure to some extend limit the dispersal of individuals.

At Kipuka Puaulu, HVNP carried out extensive fieldwork at the study site from 2001 to 2008, color-banded more than 100 individuals, collected blood samples, and monitored the population structure by monthly surveys, which provided great foundation for this dissertation study. Unpublished banding data and observations of the Kalij by USGS biologist Thane Pratt in HVNP over three years suggested each social group contained one female and one or multiple males, and males within a social group exhibited cooperative behaviors. Pratt proposed that the "excess male(s)" may be offspring of the breeding pair from earlier years, who help raise chicks but do not breed even though they are sexually mature after the first year (Johnsgard 1999). Alternatively, flock males may be brothers, both of which may potentially mate with the female - a polyandrous form of cooperation rarely documented. Female helpers have never been observed.

Preliminary surveys and the banding data from Thane Pratt showed very high densities at the study site. This suggests that habitat may be saturated in the population, leaving no empty habitat available for male offspring to breed independently. Consequently, they cooperate with family members. Second, even if habitat is not saturated, there may be a shortage of females in the population with whom subordinate males can establish an independent breeding group. Both limitations can prevent sexually mature offspring from leaving the natal group and establishing a breeding group on their own (Krebs and Davies 1993; Hatchwell 2007). Based on the USGS banding data, most males in a certain group grew up in the group, indicating group males may be related. However, the genetic kinship among group members is not clear.

Study Aims and Dissertation Structure

I examined the ecology of Kalij Pheasants and their cooperative breeding behavior at the study site, both through field observations and genetic analyses. I proposed and tested hypotheses on possible contributing factors to cooperative breeding behavior.

In the first chapter, I examined the population structure and group composition, social behaviors (including within-group dominance and attributive factors), cooperative breeding behaviors, and breeding ecology of Kalij Pheasants at the study site. I then discussed possible ecological and life history factors that influence cooperative breeding behavior. I also compared the cooperative breeding systems among reported cases of pheasants that cooperatively breed.

In the second chapter, I tested the hypotheses that habitat saturation and mate limitation possibly influence the cooperative breeding of Kalij Pheasants in the studied population. Because the high density in the population suggested potential habitat saturation, I removed about one-third of the social groups in the population to create vacant habitats, and recorded changes in the population including group organization. A comparison of sex ratio before and after removal was discussed in relation to possible mate limitation in the population.

In the last chapter, I examined how genetic benefits gained by helpers contributed to the maintenance of cooperative breeding in this population. I used multi-locus autosomal microsatellite analyses to 1) estimate genetic relationship among individuals within social groups, and tested the hypothesis of kin selection; and 2) estimate parentage of chicks in sampled groups, and tested the hypothesis of direct benefit. I provided the extra-pair paternity (EPP) and conspecific brood parasite (CBP) rates. I then discussed the mating system of Kalij Pheasants at the study site, and compared the EPP and CBP rates to similar bird groups. The genetic analyses in this chapter were carried out in collaboration with Dr. Yang Liu from Sun Yat-Sen University in China.

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Chapter 1: Social Behavior and Cooperative Breeding in a Precocial Species: Kalij Pheasants (*Lophura leucomelanos*) in Hawai'i

Abstract

Cooperative breeding in birds occurs mostly in altricial species, in which the offspring need substantial parental care to survive; precocial species afford unique opportunities to examine the factors influencing cooperative breeding without the constraint of extensive offspring needs. We examined social behavior and documented cooperative breeding for the first time in Kalij Pheasants (*Lophura leucomelanos*) in an introduced population in Hawai'i, a third reported instance of cooperative breeding in Phasianidae. Each social group contained one female and one to six males. All adults exhibited cooperative behavior including caring for chicks, agonistic behaviors against conspecific intruders, and vigilance against predators. Within each group, one male was dominant over the others and appeared to be the breeder. Age was the only factor found to determine within-group dominance, suggesting that subordinate males can eventually gain dominance and breeding status by staying in the group. In families with clear pedigree, most males grew up in the group, suggesting group males may be related. During this study from 2009 to 2011, the average group number was 28, and group composition remained relatively constant; the average population density was high with an average of

3.21 residents/ha, which can possibly lead to habitat saturation in this population; the adult sex ratio was biased toward male with an average of M:F = 2.10, which can possibly lead to female limitation in this population. Genetic sex identification of egg samples revealed unbiased primary and secondary sex ratios and suggests that the bias in adult sex ratio can be caused by differential survival between males and females. Recent observations of cooperative breeding in precocial species indicate it may be more common than conventionally recognized.

Keywords：

Cooperative breeding, precocial species, *Lophura leucomelanos*, social queuing, habitat saturation, mate limitation

Introduction

In birds, offspring are usually cared for by one or both parents (Cockburn 2006) in early stages of life in order to survive. In certain reproductive systems, one or more additional members of a social group may provide care to young that are not their own offspring, where the sexually mature aid-givers may or may not mate with breeding individuals; in short, where cooperative breeding occurs (Stacey and Koenig 1990). Cooperative breeding is evolutionarily significant because helpers cooperating at the expense of their own reproduction seems contrary to evolution by natural selection. However, helpers have been found to gain benefits via other mechanisms, such as mating with group members (Koenig 1981), becoming a breeder in the group at a later time (Kokko and Johnstone 1999), being helped by the offspring that they cared for earlier (Reyer 1986; Kokko et al. 2001), or from helping closely-related individuals (i.e., indirect genetic benefits) (Hamilton 1964b, a; Maynard Smith 1964; Smith and Wynneedwards 1964; Woolfenden and Fitzpatrick 1984).

Cooperative breeding in birds is relatively rare. Based on empirical studies, Brown (1987) estimated that 2.5% of avian species breed cooperatively. Based on phylogenetic inference, Cockburn (2006) estimated that cooperative breeding may occur in as many as 9% of avian species. Cooperative breeding in birds occurs mostly in altricial species (Brown 1987; Cockburn 2006), in which the substantial offspring demand for parental care of helpless hatchlings predisposes them to alloparental care, which has been suggested to play a key role in the evolution of cooperative breeding (Brown 1987; Ligon and Burt 2004). Not surprisingly, such behavior is expected to be relatively rare in precocial birds (4% of 789 species, Cockburn 2006), which lack the strong driver of intensive offspring needs. Thus, when cooperation does occur in precocial species it provides a unique opportunity to advance our synthetic understanding of the evolution and maintenance of cooperative breeding behavior. First, the potential effects of ecological factors (e.g., habitat saturation, Komdeur 1992, mate limitation, Fessl et al. 1996) and life history traits (e.g., high longevity and low annual adult mortality, Brown 1974; Ricklefs 1974; Arnold and Owens 1998) can be examined in precocial species without the influence of substantial offspring demand, and it may reveal clearer cost-benefit relationship (such as dominance and reproductive skew among group members) between these factors and cooperative breeding. Second, the physiology and life history of precocial species are quite different from those of altricial species along the gradient of precociality, and this can offer higher variation in these characteristics and subsequently increase the power of interspecific comparative analysis as detailed studies of cooperative breeding in precocial species accumulate. For instance, interspecific comparative analysis across altricial and precocial birds suggested that prolonged offspring dependence in terms of the duration of postfledging offspring care was significantly longer in bird species that regularly breed cooperatively (Langen 2000), but information on postfledging parental care in precocial species is scarce for testing such hypothesis.

Here we document social behavior and cooperative breeding behavior in a recently established population of Kalij Pheasant (*Lophura leucomelanos*) in Hawai'i Volcanoes National Park. Like all pheasants (Galliformes: Phasianidae), Kalij Pheasants are precocial, thus providing an opportunity to study cooperative breeding removed from its usual association with altricial young. As a family, pheasants exhibit monogamy, polygyny and promiscuity (Johnsgard 1999). In a phylogenetic reconstruction based on Sibley and Ahlquist (1990), Arnold & Owen (1998) suggested that cooperative breeding had never evolved in phasianids. Likewise, using phylogenetic inference Cockburn (2006) predicted that cooperative breeding would be absent in Phasianidae. Substantial sexual dimorphism and showy traits in males of most pheasant species (Beebe 1918) also suggest strong sexual selection on males, making cooperative breeding among males less likely. However, the mating and breeding system of phasianids may be more plastic than expected. Two likely occurrences of cooperative breeding in phasianids have been recently recorded in the Buff-throated Partridge *Tetraophasis szechenyii* in Sichuan, China (Xu et al. 2011) and in a population consisting of hybrids between the White

Eared-Pheasant (*Crossoptilon crossoptilon*) and the Tibetan Eared-Pheasant (*C. harmani*) in Tibet, China (Lu and Zheng 2005).

Based on field observations by Thane Pratt, Kalij Pheasants in our study population in Hawai'i manifest a social group structure consisting of one female with multiple males, all of whom appeared to participate in defending against conspecific individuals outside of the social group and rearing the social group's chicks. This provides a unique opportunity to examine the likely cooperative breeding in a precocial species in a new environment, and the factors influencing that behavior. We examined the ecology of cooperative breeding of Kalij Pheasants at the study site, including population demography and group composition, cooperative behavior and dominance among group males, as well as their breeding ecology. Population demography such as density and sex ratio can reveal the condition of ecological factors in this cooperative breeding system, and life history examination can shed light on longevity and group turnover rate in this population that may contribute to cooperative breeding.

Methods

Study-site

Most of the work we report was conducted from January 2009 to July 2011 at the Kipuka Puaulu forest (19°26' N, 155°18' W) in Hawai'i Volcanoes National Park (HVNP) on the Island of Hawai'i, USA. “Kipukas” are older growth forested vegetation surrounded by relatively recent lava flows, creating a semi-isolated habitat for forest-dwelling species such as Kalij Pheasants. Kipuka Puaulu is 42 ha of disturbed native Hawai'ian forest surrounded by lava rock fields with scattered shrubs and trees located around 1200 meters elevation on the southeastern flank of Mauna Loa volcano. The mean annual temperatures are uniformly around 16°C, with a difference of about 3.5°C between August and February means; annual rainfall is approximately 1500 mm, varying monthly from about 25 mm in June to 200 mm in January (Mueller-Dombois and Lamoureu 1967). The forest is three-layered, with the dominant trees being 'ohia lehua (*Metrosideros polymorpha*), koa (*Acacia koa*), manele (*Sapindus saponaria*), olopua (*Nestegis sandwicensis*) and pilo (*Coprosma rhynchocarpa*). The intermediate layer contains mainly the dominant shrub mamaki (*Pipturus albidus*) and native tree fern 'ama'u (*Sadleria cyatheoides*), and the understory consists of native ferns (such as kupukupu *Nephrolepis exaltata* ssp. *hawaiiensi*), vines (such as Maile *Alyxia stellata*) and invasive grasses (such as meadow ricegrass *Ehrharta stipoides*). This study focused on a core area of 27 ha inside and around a loop trail in the forest. Kalij in this core area have been studied episodically since they first arrived there in the 1970s (T.K. Pratt, unpubl. data; Pratt 1976; Lewin and Lewin 1984).

Study-species

Kalij Pheasants are native to south Asia, where it is comprised of nine morphologically distinct and geographically separated subspecies (Johnsgard 1999). It occurs mainly on the west side of the Himalaya Mountains across various habitat types, from mountainous forests to lowland cultivated lands and forests, depending on subspecies (Barnes 1981). Its basic ecology and behavior have not been intensively studied. Previous studies conducted in their natural range and habitat (Baker 1930; Ali and Ripley 1969; Delacour et al. 1977; Gaston 1980; Barnes 1981; Iqbal 1992; Johnsgard 1999) and in Hawai'i (Lewin and Lewin 1984) suggest that the mating system of Kalij Pheasants can be monogamous or polygynous based on their group composition during breeding season, but these sources make no mention of cooperative breeding. Curiously, Iqbal (1992) reported that while the majority of sightings included male-female pairs, occasional sightings revealed groups expressing a variety of compositions such as 2 males and 1 female, 1 male and 2 females, before, during and after the assumed incubation period of females in the breeding season. Iqbal (1992) also suspected that Kalij Pheasants form wintering flocks. Johnsgard (1999) reported that birds assume adult plumage and are able to breed the year following hatching.

The Hawai'ian population is a hybrid of two subspecies: the white-crested Kalij (*L. l. hamiltoni*) and the dark-crested Kalij (*L. l. leucomelanos*) (Pratt 1976), and individual phenotypes are quite variable. The Hawai'ian population was introduced onto the Pu'u Wa'awa'a Ranch of the island in 1962, established with 67 birds collected from Michigan and Texas game farms; the entire island population is believed to have originated from these 67 individuals (Swedberg 1967; Lewin 1971). They have flourished since then and were reported to have become widely distributed in various types of forests from sea level to 2450m elevation on the island by 1984 (Lewin and Lewin 1984). A later study suggested that their range was still expanding (Reynolds et al. 2003). They reached our study site in HVNP in the 1970s, increased in the 1980s, and have been abundant since the 1990s (T. K. Pratt, unpubl. data).

Trapping, tagging, radio-tracking and genetic sampling

From 1999 to 2011, we used walk-in traps and drop traps (modified from Aruch et al. 2003) to catch Kalij Pheasants. HVNP banded more than a hundred individuals in Kipuka Puaulu from 2000 to 2004, and our field crew banded 66 individuals from 1999 to 2011. Although some of these individuals disappeared from the population through time, about 85% of the ~90 resident individuals in the core area were uniquely metal- and color-banded during this study, allowing individual identification by resighting. We captured each individual once and conducted capturing between 8 am and 7 pm. The same person measured body mass and morphological characters at capture, and collected a blood sample of approximately 100 µl from the brachial vein, which we preserved in 99.5 % ethanol at −20 ˚C within a few hours of collection. We measured body mass using a spring scale to the nearest 0.01 kg, measured tail length, wing length and tarsus length using a ruler to the nearest 1 mm, and measured spur length and beak length using a caliper to the nearest 0.1 mm for each individual.

We radio-tagged 15 females in order to locate their nests in the breeding season. We used 2477 Pheasant Necklace Module collar transmitters from AVM Instrument Company, a 3-element Yagi tracking antenna, and a TRX-1000 radio receiver from Wildlife Materials Inc. We located 17 nests by following females with radio transmitters during their nesting period from 2009 to 2011. We collected 92 egg membranes and unhatched embryos from those nests, and preserved them in 99.5 % ethanol at −20 ˚C within a few hours of collection.

We carried out fieldwork including capturing, banding, radio-tracking and genetic sampling of Kalij Pheasants under Protected Wildlife Permit No. WL010-06 (Department of Land & Natural Resources, State of Hawai'i, USA), Scientific Research and Collecting Permit No. HAVO-2010-SCI-0025 (National Park Service, U. S. Department of the Interior), and Animal Care and Use Protocol No. A-20080047 (University of California, Riverside).

Population Structure and Group Composition

From January 13 to February 21, 2011, we conducted population and group composition surveys by walking 30 transects twice a week, collecting data between 6:30 am and 6:30 pm. The 30 transects, which were 25 meters apart, lie east-west across the study area. We recorded all sightings of individuals encountered and the composition of social groups. We recorded geographic coordinates of each sighting using a Garmin eTrex Legend HCx Geographic Positioning System accurate to the nearest 0.001 minute. Every resident group in the core area was recognizable using band combinations and unique physical characteristics of unbanded members, including crest color and length, nape color, rump color, breast color, and spur color, length, and shape. Individuals seen in close proximity (less than 2 meters from each other) without aggression for 3 or more times were considered to be part of the same social group. In addition to resident groups that defend their territory year-round, we also recorded sightings of floater males and females (non-group affiliated individuals).

Determination of Dominance and Influencing Factors

Between January 13 and February 21, 2011, we conducted behavioral surveys on all groups with more than one male to assess within-group dominance. The observer stood approximately 3 meters from the flock, providing 10 grams of dry cracked corn at min 0, 2, 4, 6 and 8 at a certain location when all group males were present to stimulate agonistic behavior among them. Each survey lasted 10 min. We used focal sampling (Lehner 1998) on the following three behaviors: pecking (one individual pecks the other, resulting in the retreat of the other), displacement (one individual rapidly approaches the other, resulting in the retreat of the other) and avoiding (one individual quickly remove its body parts such as the head and neck away from the other individual, sometimes accompanied by one or two steps away from the other individual). Male A scored the interaction if male A pecked or displaced male B, or if male B avoided male A. We designated male A to be dominant over male B when male A scored 3 times or more. In groups with more than two males, we determined the one male that was dominant over every other male as the dominant male of the group. No reversal or triangular relationships were recorded during this study.

Social dominance status can be related to age of animals (Wilson 1975), such as in White-throated Sparrows *Zonotrichia albicollis* (Piper and Wiley 1989) and Dark-eye Juncos *Junco hyemalis* (Holberton et al. 1990), or morphological characters, such as body mass in the Red Jungle-fowl *Gallus gallus* (Zuk et al. 1998). We identified the age of individuals using banding data from HVNP and from our study. For example, if an individual was banded between May 2001 and April 2002 as juvenile, indicating it was hatched in 2001, we determined its age in 2002 as 1; if an individual was banded between

May 2001 and April 2002 as adult with unknown age, we determined its age in 2002 as “at least 2”. To test if age influenced social dominance in this Kalij Pheasant population, we compared 1) the age of dominant to subordinate males within all social groups (relative age) in which the ages of all males were known; and 2) the ages of all dominant males to all subordinate males from those groups (absolute age). In this analysis, we considered the age of an individual as 2 if its age was determined as "at least 2. To test if size influenced social dominance, we used a multivariate model GLMM (generalized linear mixed model) to analyze the relationship between dominance status and individual morphological measurements. In the GLMM, we treated dominance status as the response variable with 1 for dominant male and 0 for other males. Among the morphological measurements including body mass, tail length, wing span, tarsus length, spur length and beak length, only body mass and tarsus length were highly correlated (Pearson correlation, $r = 0.63$, $P < 0.001$, $n = 35$); therefore we used body mass (and not tarsus length) and the other measurements as explanatory variables. We included group identity as a random factor to account for the non-independence of individuals within a group.

Cooperative behaviors

Unlike altricial birds, in which cooperative behavior can be readily quantified by assessing food provisioning rates at the nest by different individuals, the care of precocial species mainly includes more generalized behaviors in the after-hatch to before-fledging period (Du Plessis et al. 1995), such as calling chicks over for food. We recorded cooperative behaviors among males (defense against intruders or predators and cooperative parenting behavior exhibited by both males and females) opportunistically as encountered using *ad libitum* sampling, which is to say, we recorded any behavior of any individuals that appeared relevant to the observer (Lehner 1992) from January to July 2011. Time and location were recorded, and behavioral descriptions were taken from beginning to end of each target behavior. A total number of each type of behavior was counted, but the frequency was not calculated due to the qualitative nature of *ad libitum* sampling.

Breeding ecology

The observed courtship displays in male Kalij Pheasants include the “tail-fanning” and “run-jump” displays described by Lewin and Lewin (1984). In “tail-fanning” the male turns sideways and fans his wing and tail feathers towards the female while walking around her; in “run-jump” the male runs towards the female from several meters away followed with up to four jumps. We recorded these courtship behaviors of males non-systematically as encountered using *Ad libitum* sampling method (Lehner 1998) in

2011. Time and location were recorded, and behavioral descriptions were taken from beginning to end of each target behavior.

From 2009 to 2011, we located nests of radio-tagged females using radio-telemetry. We measured egg mass to the nearest 0.1 g and the egg’s long and short axes to the nearest 0.01 mm. Because eggs were found to lose $\overline{x} \pm SE = 13.2\% \pm 4.54\%$ ($n = 9$, 1 nest) of their weight over the incubation period, we only used weight measurements taken within 2 days after incubation began. Hatching rate was calculated using the number of hatched eggs divided by the number of eggs laid in a nest. Unhatched eggs were examined by eye and under the microscope, and considered fertilized if tissues of embryos were found. We calculated fertilization rate from these data. We placed a Bushnell® Trailscout motion-sensing infrared digital trail camera 1.5 meters from a nest from May 17 to June 11 in 2010 to document the incubation behavior of a female.

Sexing offspring

We extracted the total genomic DNA from egg tissue samples using TianGen Biotech DNA extraction kits DP318, and stored extracted DNA at -20°C within a few hours of collection. We used the primer set 2550F/2718R (Fridolfsson and Ellegren 1999) to amplify DNA fragments to establish the sex of an offspring. 2550F/2718R amplifies an approximately 600 bp fragment on the Z chromosome-linked CHD1Z gene, and an approximately 450 bp fragment on the W chromosome-linked CHD1W gene in non-ratite birds, including pheasants. Therefore, amplification products show one fragment in males, and two fragments in females.

We performed PCR amplifications in a 10 µl reaction mixture containing 5 µl Takara Bio PerfectShot® Ex Taq (loading dye Mix), 20 ng genomic DNA, and 0.1 µM forward and reverse primers. We performed the reactions on Invitrogen Applied Biosystem® Veriti™ Dx 96-Well Thermal Cycler with the following conditions: 5 min at 94°C, 17 touch-down cycles consisting of 30 sec from 52°C to 43°C (decreasing by 0.5°C each cycle), 3 min at 57°C, and 45 sec at 72°C, then 5 min at 94°C, 40 sec at 43°C, and 45 sec at 72°C, followed by an ending temperature at 4°C. We separated amplified PCR products in 5 µl reaction mixture by agarose gel (2%) electrophoresis, visualized target band using Invitrogen SYBR® Green I nucleic acid stain, and used Takara Bio DL2,000 DNA Marker as a size reference.

Results

Population Structure and Group Composition

Population surveys documented and monitored all resident individuals at the 27-ha core area from 2009 to 2011 (Table 1.1). Density in the population was high, and the adult sex ratio (ASR) was biased towards males. The number of social groups in the core area remained similar across the three years. Reproductive success was high in 2009, resulting in a large number of juveniles (28M, 19F) in the population at the beginning of 2010. Consequently, resident numbers increased in 2010 and 2011, and the proportion of multiple-male groups was slightly higher. From March 11 to April 26, 2010, all 19 female juveniles and 2 male juveniles disappeared from their social groups, most likely due to dispersal, resulting in a significantly male-biased ASR in 2010 (Fisher's exact test, $p = 0.0049$) and 2011 (Fisher's exact test, $p = 0.0104$). The 26 juvenile males in the population remained in their natal groups. Reproductive success was low in 2010, and no juvenile was recorded in resident groups in the core area in 2011.

Males always rejected non-group males when encountered. However, in all 16 multi-male groups with a known field pedigree from among the 20 total multi-male groups that occurred at the study site from 2009 to 2011, some males that grew up in the group stayed in the group after reaching adulthood. Therefore group males were likely related (for example, father-son, uncle-nephew or brothers) under the circumstances when all offspring were sired by the same parents in a group. Female offspring always dispersed before the group female nested in the subsequent breeding season (17 events in all 8 groups recorded to have female offspring from 2009 to 2011).

Table 1.1. Population structure in May, 2009-2011

Year	Residents/ha	# Resident M	# Resident F	Adult Sex Ratio M/F	# groups w/ 1M	# groups w/>1M
2009	2.70	45	28	1.61	13	14
2010	3.56	68	28	2.43*	11	17
2011	3.37	63	28	2.25*	12	17

*Statistically different from 1.0 (Fisher's exact test, $p < 0.05$).

Kalij Pheasants in the studied population formed stable social groups with cohesive group composition year-round and across years. From 2009 to 2011, there were 28, 28 and 29 groups, respectively, in the study area (Table 1.1). Groups generally remained the same area except for the dispersal of offspring and some exceptions discussed below, including 5 cases of groups shifting in or out the study area, 6 cases of adult disappearance likely due to mortality, 3 cases of change of the group female, and 3 cases of group division.

Between 2009 and 2010, we recorded the following changes: 1) One 1M1F group banded in 2002 within the study area, which had shifted outside the study area, later moved back into the north boundary of the study area in 2010. 2) One 3M1F group that was not previously recorded at the study area moved into the southwest corner of the study area in 2010. 3) One 1M1F group at the southeast corner of the study area in 2009 shifted outside the study area in 2010. 4) One single female that was at least 10 years old disappeared possibly due to mortality. This female and her previous group had been recorded in the studied area since 2000. Her mate disappeared between 2008 and 2009, and the female alone stayed in the same area in 2009 without obtaining a new mate. 5) An 8-year-old male of a 2M1F group disappeared possibly due to mortality. 6) The females of two groups at least 8 and 10 years old, respectively, disappeared possibly due to mortality. Both groups obtained a new female soon after. In one case the new female was observed only one day after the previous female disappeared.

Between 2010 and 2011, we recorded the following changes: 1) One 5M1F group that was not previously recorded at the study area moved into the northeast corner of the study area in 2011. 2) One 3M1F group at the southeast corner of the study area in 2010 shifted outside the study area in 2011. 3) In each of two groups, a 2-year-old male offspring left his previous group and obtained a new female in an area near his previous group. 4) An at least 13-year-old male was evicted by the younger males in his previously 3M1F group. The old male was chased away in every encounter by males from its old group but stayed in the same area and still fought other intruders. He did not obtain a new female. 5) In a previously 3M1F and a previously 5M1F group, the oldest males (9 years old and at least 13 years old, respectively) disappeared possibly due to mortality. 6) The female, at least 2 years old, in one 1M1F group disappeared, and the group obtained a new female.

Group members predominantly stayed together during the day (observations from all 31 groups at the study site from 2009 to 2011) and predominantly roosted on the same or nearby trees at night (recorded in all 16 groups observed from 2009 to 2011), except for during the nesting period when the group female was absent from the group (recorded in all 11 groups with breeding attempt in 2011). Each group maintained a relatively constant home range year round, with large overlap among neighboring groups (L. Zeng, unpubl. data). Every social group contained 1 female and 1 to 6 males, except for one group in 2009 that only contained one female at least 8 years old (an individual who had stayed around the area for at least 8 years although her mate disappeared in 2009), and one group in 2011 that only contained one male at least 12 years old (an individual evicted by his previous group members but that still stayed in the same area and fought intruders from other groups) with no female. From 2009 to 2011 there were always more groups with multiple males than groups with one male (Figure 1.1).

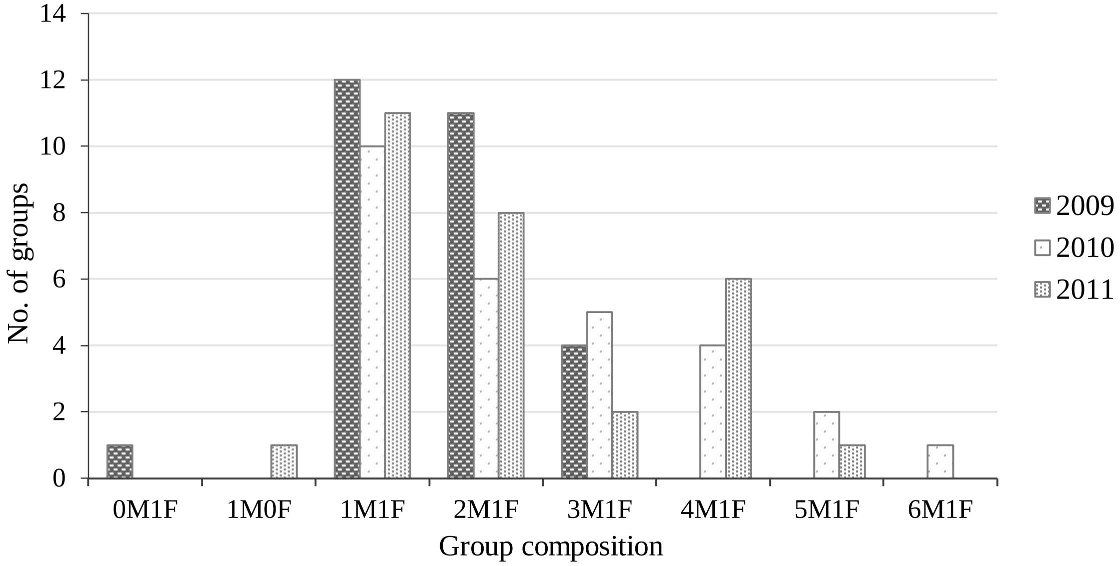

Figure 1.1. Social group composition in our study population of Kalij Pheasants on the island of Hawai'i from 2009 to 2011.

All males within a social group for whom we had a pedigree (Pratt and Zeng, unpubl. data) grew up in the same group, indicating that within-group males could be related as brothers, father-son or uncle-nephew. The genetic relationship among group males is not certain due to complications such as potential extra-group paternity and chick-mixing between groups. We observed chick-mixing three times in two groups in 2011, confirmed by an increase in chick number more than two weeks post-hatching. In one incident, the group female sat on chicks of the group when a non-group female was present with her chicks, possibly in order to prevent chick-mixing. All group members traversed, foraged, and roosted together with rare exceptions.

We also recorded floaters each year. In 2011, we recorded 45 male floater sightings and 25 female floater sightings out of 2469 total sightings, including both resident and floater sightings. Because floaters were more skittish and harder to see than residents, it is likely that floaters occurred more frequently than we have recorded.

Dominance and Influencing Factors

We collected behavior data on 16 of the 17 groups with more than one male to determine intra-group dominance. We recorded a total of 85 events (2.36 ± 1.33 events per dyad) of target behaviors between 38 dyads in the 16 surveys. We did not observe any reversal of dominance in the target behaviors, indicating the target behaviors were stable indicators of dominance. We also recorded 34 events of the target behaviors among 22 dyads during non-survey fieldwork without artificial food provisioning from January to July 2011, and all events were consistent with survey results, indicating that the dominance relationships within a group are likely stable year-round.

In 13 of the 14 groups (38 males) for which we determined dominance and age among males, the dominant male was older than subordinate male(s), suggesting age is a factor determining within-group dominance status. In the only exception, the dominant and subordinate males were of the same age.

The absolute ages of dominant and subordinate males in these 14 groups are not statistically different as some groups contained old subordinate males that were close in age to the dominant male, and in some groups all males were relatively young. However, dominant males ($\bar{x}$ ± SE = 7.79 ± 2.83) had a higher average age than subordinate males ($\bar{x}$ ± SE = 3.83 ± 2.62) (Figure 1.2).

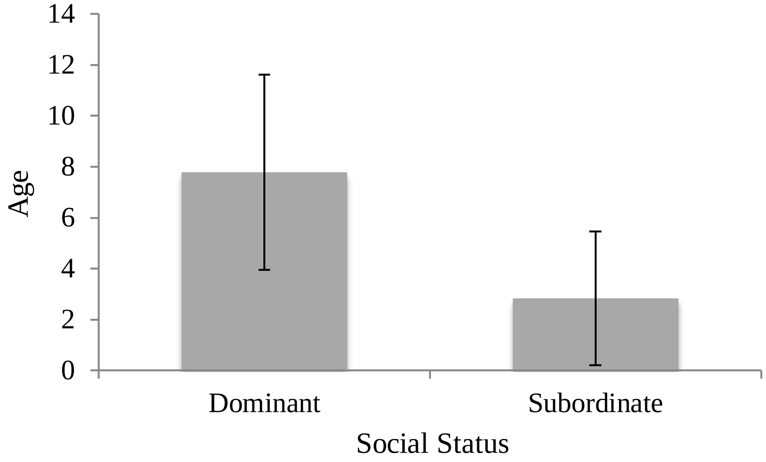

Figure 1.2. Age of 14 dominant and 24 subordinate males in 14 groups with age determined for all males.

In the 13 groups (n=35 males) for which we determined dominance among males and measured morphological characters for all males, none of the morphological measurements was significantly associated with dominance status (Table 1.2).

Table 1.2. Generalized linear mixed model (GLMM, F = 1.036, df = 1, 29, p=0.42) showed none of the morphological measurements of males was significantly associated with dominance status.

Factors	F	df	P
Body mass	0.001	1,29	0.98
Beak length	0.936	1,29	0.34
Spur length	0.942	1,29	0.34
Tail length	3.150	1,29	0.09
Wing length	0.622	1,29	0.44

Cooperative breeding behaviors

Cooperative breeding behaviors were documented within social groups, including agonistic behaviors against conspecific intruders, being alert and defending against predators, and caring for chicks.

1) Agonistic behaviors against conspecific intruders. Both sexes exhibited strong agonistic behavior towards intruders of their own sex, including individuals from adjacent groups, as well as floaters. Behaviors we identified as agonistic included long and high-pitched alarm calls, clusters of relatively low-pitched aggressive calls, pecking, chasing, and jumping forward while extending legs and spurs towards intruders. Agonistic behaviors always occurred when different groups approached within approximately 10 meters, and it seemed to usually start immediately when one group came into sight of the other group. We recorded at least some if not all of the above agonistic behaviors in every group male in all groups. The female of the social group also fought intruder female(s) using the same behaviors, except that females do not possess spurs. In 2011, agonistic behaviors between different groups were recorded 97 times, including 63 times among males and 28 times between females. In 6 instances, male(s) initiated agonistic behaviors toward the female of the other group, and it was not clear if such behaviors serve territorial or courtship purposes in such encounters.

2) Defending against predators. Potential predators for adults, chicks, and eggs included mongoose (*Herpestes javanicus*), feral cat (*Felis catus*), 'Io (or Hawai'ian Hawk, *Buteo solitarius*), Pueo (or Hawai'ian Short-eared Owl, *Asio flammeus sandwichensis*), Barn Owl (*Tyto alba*), and domestic dog (*Canis familiaris*). All adults exhibited vigilance in the presence of predators, including watching out for predators, making single-note contact calls, high-pitched alarm calls, and clusters of aggressive calls. We did not observe any fighting against predators, with one exception where the female from a group ran towards a mongoose when the group was with small chicks.

3) Parenting behavior. Food provisioning was recorded in all but one of 30 adults, male or female, in all 11 groups with chicks. Such behavior included making “food calls” (see Evans and Evans 1999) and adults pointing their beaks at food such that chicks came over to feed, as well as picking up food items and feeding them directly to the chicks. The only exception was a subordinate male of a group who not only did not provision food to the chicks of the group, but was also recorded 3 times to peck and chase the chicks. The dominant male of the group always intervened by initiating agonistic behaviors towards the subordinate male, which always resulted in the subordinate male stopping the harassment of chicks and leaving. In another case, an intruder male chased the chicks of the group and the dominant male of the group intervened by initiating agonistic behaviors towards the intruder male.

The group female was observed 5 times in 4 groups covering chicks under her body and wings when there were signs of predators, or when it was cold or rainy. We observed 11 roosting events in 4 groups with chicks. Before chicks were approximately two weeks old, the group female stayed on the ground to roost with chicks at night at the base of trees covered by some ground vegetation, covering them with her body and wings. After about two weeks post-hatching, the female led chicks to roost on the same tree with group males by jumping up the branches. In 4 cases recorded, all chicks tightly roosted together on a branch next to or near the group female. In one case, a chick roosted next to a group male.

Breeding ecology

We observed courtship displays, including the lateral display and “rum-jump” display. In 2011, courtship was recorded once in January, once in March and 8 times in April. Four of the observed courtship displays were from the oldest male of the female’s group to the female, 2 were from the younger male of the female’s group which consisted of 2 males, and 6 were from the oldest male of an adjacent group. In both 2 cases where the younger male of the group courted the group female, the older male intervened to prevent him from approaching the female. The youngest male to establish a breeding group alone with a female who successfully produced chicks during this study was 2 years old.

Females incubated eggs mainly from April to July, with a small variation between years. In 2009, 7 females incubated eggs between May and June, 5 of which most likely lasted only through May. In 2010, 6 females incubated eggs between May and June, and 1 female was found sitting on nest in August. In 2011, 10 females incubated eggs between April and May, and 1 female incubated eggs between May and June. No multiple nesting attempts by the same female within a season were recorded during this study. The only incubation period confirmed to the day was 26 days, which was longer than previously documented (20-22 days, Baker 1930; 23-24 days, Delacour 1977; 24-25 days, Ali and Ripley 1969).

In 4 instances, we recorded a new female staying together with the group males during the incubation period of the group female; the new female stopped associating with the group males after the group female returned from the incubation period.

Females incubated eggs alone, and group males were never recorded in proximity (within 5 meters) to the nest. At the 17 nests observed, females sat on the nest to incubate, covering all eggs with their body and feathers. At the nest monitored by infrared camera, the female used feet and beak to shuffle the eggs every half hour to one hour, with higher frequency at night. The monitored female left the nest to forage once or twice a day, mostly in the early morning and/or afternoon for one to two hours, with the morning off-bout longer than the afternoon one. In 5 mornings that we were near the nest when she left the nest, we observed her making a long (3~4s) high-pitched whistling call immediately after she left the nest, after which the group males came over to reunite with her and they foraged together. The infrared video camera footage showed that after hatching, chicks did not leave the nest immediately, but stayed with the female at the nest for a day without feeding, and left the nest to join the group males with the female in the second day.

Among 20 nests located, 7 were at the base of a large fallen log where it contacted the ground, 5 were in dense thickets, 5 were in tall grass, 2 were on top of a large fallen log (one on the root part 1.5 meters above ground, one on the trunk part 1.1 meters above ground) and 1 was in the low crotch of a big tree 1.3 meters above ground. Among 20 nests, 15 were within the home range of the group, 3 were outside of the home range, and 2 were unidentified with respect to the home range (L. Zeng, unpubl. data).

The clutch size ranged from 5 to 11 (7.47 ± 2.24, n = 17). The fertilization rate was 92.76% ±19.35% (n = 13), and the hatching rate was 99.23% ± 2.77% (n = 13). The long axis of eggs was 46.9mm ±1.52mm (n = 35, 5 nests), and the short axis was 35.3mm ± 0.90mm (n = 35, 5 nests). Egg weight measured from a nest within 2 days of hatching was 32.9g ± 1.21g (n = 9, 1 nest), and egg weight measured from nests with unknown date of hatching was 30.4g ± 2.06g (n = 26, 4 nests).

Primary and secondary sex ratio

We estimated the primary sex ratio using fertilized eggs (including hatched and unhatched ones) from 17 nests. Among the 92 sexed offspring, 47 were male and 45 were female, resulted in a primary sex ratio of M:F = 1.04:1, not significantly different from 1:1 (Fisher's exact test, $p \approx 1.00$). The secondary sex ratio was M:F = 1.02:1 (46 males and 45 females at hatching), which was also not significantly different from parity (Fisher's exact test, $p \approx 1.00$). For clutch size, fertilization and hatching rate, and sex of offspring in breeding groups, see Supporting Information Table S1.1.

Discussion

Kalij Pheasants in our study population demonstrated a suite of behaviors consistent with cooperative breeding. They occurred in social groups with supernumerary individuals (in this case, excess males) who appeared to have grown up in the social group. In each group with multiple males, the dominant male was predominantly the older male, who appeared to prevent other males from courting the group female. All males, including subordinates, assisted in chick-rearing. This breeding system likely represents a recently arisen novel adaptation under new ecological conditions for this species. Cooperative breeding is extremely rare in precocial birds (Du Plessis et al. 1995; Cockburn 2006). To our knowledge, cooperative breeding behavior by Kalij Pheasants is only the third instance of cooperative breeding reported in Phasianidae, which is the largest family of the precocial order Galliformes.

Cooperative breeding in Phasianidae

The first case of cooperative breeding in Phasianids was reported by Lu and Zheng (2005) in a hybrid population of the White Eared-Pheasant and the Tibetan Eared-Pheasant. While mostly single individuals and pairs were recorded during nesting period, flocks consisted either single brood with parents and nonbreeders or mixed broods with multiple pairs of (presumable) parents and nonbreeders during late brood-rearing period. All flock-affiliated nonbreeders were male; some nonbreeders were observed to take part in feeding the young and alarm calling against predators, similar to the Kalij Pheasants we studied. Interestingly, circumstantial evidence suggests that cooperative young-care possibly exists in at least two of the four species of eared-pheasants: in the White Eared-Pheasant, Jiang (1979) observed a communal-roosting flock of up to 60 birds during the early brood-rearing period; in a population of Brown Eared-Pheasants *C. mantchuricum*, Liu et al. (1991) observed 38% of the social units contained more than one brood together with subadults. The cooperative young-caring in the White × Tibetan population and possibly other eared-pheasants can be related to the typical life history transition from monogamous pair bonds during the mating period to large winter flocks in the genus *Crossoptilon* (Johnsgard 1999; Lu and Zheng 2005).

In the Buff-throated Partridge population studied by Xu et al. (2011), 44 of 68 social units contained the breeding pair and up to three helpers of either sex (predominantly male) while the rest contained only the breeding pair. All adults of a social unit brooded chicks under their abdomens and wings, and exhibited vigilance against predators and defense against conspecific intruders. Breeder males were only observed to fight intruders when helper males were defeated by an intruder male. Similar to the Kalij Pheasants at our study site (as discussed below in the section of life history characteristics), the rate of group turnover and individual disappearances were low. No evidence suggested differences in reproductive success between unaided and aided social units.

Other than phasianids, in the Galliformes some form of cooperation has also been reported in Odontophoridae (new world quails). Communal brood-rearing was observed in Northern Bobwhite *Colinus virginianus* (Brooks and Rollins 2007), California Quail *Callipepla californica* (Lott and Mastrup 1999), Gambel’s Quail *Callipepla gambelii* (Brown et al. 1998) and Marbled Wood-Quail *Odontophorus gujanensis* (Skutch 1947). In the Northern Bobwhite population, combined broods can be cared for by multiple females only, multiple males only, or a combination of females and males. In California Quail, while most broods were reared by their parents alone, 23 out of 195 broods were reared communally by all their living parents in combined neighboring broods. Parents of combined broods lived longer and hatched more young in a lifetime than parents of single broods, possibly due to increased foraging opportunities and reduced predation. Similar forms of communal brood rearing have been observed in some non-galliform precocial birds such as Canada Goose *Branta canadensis* (Sherwood 1967) and Barrow's Goldeneye *Bucephala islandica* (Eadie and Lyon 1998). This, possibly similar to the eared-pheasants, might be a more common form of cooperative breeding in precocial species. Different from the communal brood-rearing in other quails, in Black-breasted Wood-Quail *Odontophorus leucolaemus* (Hale 2006), groups reared single broods and reproductive success increased significantly with group size, indicating that reproductive success was possibly enhanced by cooperative breeding. Groups contained 4 adults on average with sex and age not clear in all groups; groups persisted from one year to the next, often at the same location.

The above studies suggest that cooperative breeding in precocial species, regardless of the form of communal breeding or helper-at-the-nest as classified by Brown (1987), manifests itself as feeding fledglings (Du Plessis et al. 1995). As most incidences of cooperative breeding in precocial species have only recently been revealed by close examination of social behavior, it may be more common than has been recognized in the past. Failure of previous research to recognize its frequency is possibly explained in part by the conventional preconception that cooperative breeding is less beneficial in precocial species as well as the lack of detailed observations.

Kalij Pheasants in our studied population exhibited cooperative breeding in the form of helpers-at-the-nest. Each group contained 1 female and 1 to 6 males, and all adults exhibited defense against conspecific intruders as well as predators, and provided parental care to the offspring when chicks were present. More cooperative groups than pairs existed in the population. Group members predominantly moved together. Group composition was stable with little change between years, and groups persisted across the three years of study at the same area with little shift in home range (L. Zeng, unpbl. data). All males within a social group for whom we had a pedigree grew up in the same group, indicating the relationship among group males can be brothers, father-son or uncle-nephew. Male dominance was stable within groups and was likely determined by age. Although ASR was biased towards the male, both primary and secondary sex ratios did not deviate from 1:1.

Habitat Saturation

Breeding habitat is said to be saturated when suitable habitats required for successful breeding (such as food resources and nest sites) are fully occupied, and surplus young birds can only stay in the natal site. Habitat saturation as an ecological constraint can prevent offspring (male offspring in this case) from leaving the natal group and establishing a breeding territory in available habitats. This condition can contribute to offspring delaying dispersal and subsequently providing help to family members (Selander 1964; Brown 1987; Komdeur 1992).

Compared to documented density of Kalij and other pheasants in the genus *Lophura* in their natural habitat (Table 1.3), resident density was high at our study site (2.70-3.56 residents/ha) and delayed male offspring dispersal was frequently observed, suggesting that available habitat might be saturated and sexually mature offspring could be prevented from establishing new breeding groups due to lack of suitable habitat. Moreover, floaters of both sexes were recorded during the study, further supporting the likelihood of habitat saturation in this population.

Table 1.3. Density of *Lophura* pheasants in their natural habitats

Species	Individuals /ha	Literature
L. leucomelana	0.51	*(Ahmed and Khan 2013)*
	0.31	(Fleming and Bangdel 1976)
L. nycthemera	0.15	(Round and Gale 2008)
	0.09	(Xiong et al. 2002)
	0.20	(Gao and Yu 1995)
L. diardi	0.23	(Round and Gale 2008)

Life History Characteristics

While ecological factors can facilitate cooperative breeding in certain populations, life history traits are likely to predispose cooperative breeding. Extended life span and low annual adult mortality were found to be the key life history factors predisposing delayed dispersal and cooperative breeding in certain avian lineages (Brown 1974; Ricklefs 1974; Arnold and Owens 1998) because they lead to a lower rate of turnover in population and breeding territory, and therefore fewer opportunities for independent breeding among younger individuals. Moreover, a high survival rate of nonbreeders in a population produces a high density of potential helpers in comparison to breeders. In such situations, helping mitigates the cost of delaying reproduction, a circumstance that also facilitates cooperative breeding (Brown 1987). In addition, living in a relatively constant climate such as the tropical zone promotes year-round occupation of territories (Arnold and Owens 1998), which can lead to reduced territory turnover and saturated habitats.

Some of these life history attributes characterize our studied population. For example, the oldest male recorded at the study site was at least 13 years old, and the oldest female was at least 12 years old (due to lack of color banding before 2000 we were not able to determine male age older than 13 years or female age older than 12 years); only 3 incidents of disappearance of adult males 4 years old or older (whose disappearance is more likely due to mortality than dispersal compared to younger males) and 4 incidents of disappearance of group females were recorded from January 2009 to July 2011.

Sex Ratio and Mate Limitation

It has been argued that the skewed adult sex ratio widely found in cooperatively breeding birds (Brown 1987) might cause a "marriage squeeze" and result in the origin of helping by sons (Maynard Smith and Ridpath 1972; Reyer 1980). A male-biased ASR exists in this population of Kalij Pheasants, which could either be a demographic condition setting the stage for male cooperation to evolve, or the selective result of more offspring of the more helpful sex being produced, i.e., sex allocation biased towards males in this case ("repayment model", Emlen et al. 1986; Lessells and Avery 1987; Koenig and Walters 1999). In the latter condition, the helping sex is “cheaper” because it repays part of the costs the parents have incurred in raising them, and producing more of them is actually consistent with Fisher’s (1930) principle of equal investment in the sexes

(Pen and Weissing 2000). However, our examination of egg DNA found unbiased primary and secondary sex ratios, indicating no evidence of biased sex allocation in the population. The biased ASR in the population may have been due to a couple of factors. On the family level, some of the male offspring stayed in the natal group after reaching sexual maturity, whereas sexually mature female offspring never stayed and all dispersed from the population by the following breeding season. In fact, all 49 female offspring banded at the study site from 2001 to 2011 dispersed before the second nesting season and were never recorded again at the study site (Pratt and Zeng, unpubl. data). Although it is not clear if offspring disperse voluntarily or due to rejection by older group members, such gender disparity in offspring dispersal resulted in the heavily male-biased group composition in this population. On the population level, although we did not obtain any evidence of differential survival rate between males and females either among group members or solitary individuals, including dispersers or floaters, females likely suffered from a higher mortality rate during dispersal than the philopatric males. Philopatric males on the other hand can gain enhanced survivorship in familiar environments among family members (Emlen 1996, Jullien and Clobert 2000). If such a difference is present, it can also contribute to the biased ASR in this population. It is possible that the strongly male-biased ASR (which has not been reported in Kalij Pheasants in their native habitat) leads to a shortage of females in the population that prevents male helpers from breeding independently and subsequently promotes cooperative breeding among males. While field observation suggests that dominant males tried to inhibit subordinate males from courting the group female, genetic analysis is needed to determine if females mate monogamously with the dominant male of the group, with a subordinate male, or polyandrously with multiple males.

Queuing for social dominance

In cooperatively breeding groups, social status is important because dominant individuals share more benefits of association, such as more food or breeding opportunities (Blanckenhorn and Caraco 1992; Kokko and Johnstone 1999). Identifying factors determining dominance status can help us understand the disposition of cooperative breeding in a system. In this population, dominant males were predominantly the oldest male in social groups, and age was the only factor found to affect social dominance. This suggests that dominance in Kalij social groups at our study site is likely gained with age. It is possible that under ecological restrictions for independent breeding, such as habitat saturation or mate limitation, staying in the group and queuing for social dominance until a future opportunity for breeding independently emerges is ultimately more beneficial to subordinate males if they will likely eventually become dominant. Meanwhile, dispersers will the lose the benefits of group living, such as efficiency in finding and guarding food as well as increased vigilance against predators (Ridley et al. 2008).

In the field we recorded 3 cases in which the oldest male of the group disappeared from the population possibly due to mortality at the ages of 8, 9 and at least 13. In all 3 cases, the next oldest male became dominant in the group. Interestingly, in another case, the previously dominant male was evicted from the group by the younger and previously subordinate males when he was at least 12 years old, and the next oldest male became dominant in the new group. The previously dominant male was attacked by and avoided his previous male group-mates at every encounter, but stayed in the area and defended against male intruders from other groups and floaters. Although the dynamics of such processes are not clear, all field observations are consistent with the argument that males can gain social dominance by staying in the group until the previously dominant male becomes too old or disappears.

In conclusion, Kalij Pheasants at our study site formed stable social groups between one female and one or multiple males. One male was dominant over the others within a group, and social status was likely gained with age. All adult group members performed cooperative breeding behavior including caring for chicks. Habitat was likely saturated due to high population density, and can subsequently promote cooperative breeding among group members. While adult sex ratio was biased toward males, primary and secondary sex ratio revealed from egg samples were unbiased. It is possible that females suffered from higher mortality than males, and that female limitation contributed to the male-biased group composition. Moreover, recent close examinations of social behaviors in Galliformes indicate that cooperative breeding may be more common in precocial birds than traditionally comprehended. The benefits and costs of breeders and helpers along with factors influencing such behavior shall provide special insights to the evolution and maintenance of cooperative breeding.

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Supporting Information

Table S1.1. Clutch size, fertilization rate, hatch rate, primary and secondary sex ratio based on 92 offspring of 17 nests sampled from the population from 2009 to 2011.

Nest	Clutch size	No. fertilized	Fertilization rate	No. hatched	Hatch rate	No. sexed	No. males	No. females
1A09	7	2	29%	2	100%	2	0	2
WT09	7	7	100%	7	100%	7	2	5
BC09*	6					2	0	2
TT09	10	10	100%	10	100%	7	2	5
DB10	9	9	100%	9	100%	9	6	3
BC10	5	4	80%	4	100%	4	4	0
S110**	8					1	0	1
1A10**	8							
TT10	5	5	100%	5	100%	5	2	3
WT10**	5							
1A11	8	8	100%	8	100%	8	2	6
CS11	3	3	100%	3	100%	3	3	0
DB11	10	10	100%	9	90%	10	5	5
H311	10	9	90%	9	100%	9	5	4
IV11	11	11	100%	11	100%	11	7	4
S311	6	6	100%	6	100%	6	4	2
WT11	9	9	100%	9	100%	8	5	3

* represents abandoned nest, and ** represents predated nests.

Chapter 2: Habitat Saturation Contributes to the Cooperative Breeding of the Kalij Pheasant (*Lophura leucomelanos*) in Hawai'i

Abstract

Cooperative breeding in birds occurs mostly in altricial species, in which the helpless hatchlings require extensive care. By contrast, cooperative breeding in precocial species is rare and hardly studied in detail. However, examining cooperative breeding in precocial species can fill a gap in understanding how ecological factors influence cooperative breeding without the substantial needs of offspring. Habitat saturation and mate limitation are two ecological constraints most commonly found and examined in cooperative breeding species. If tested in precocial species, it will make a stronger case as attributing factors for cooperative breeding. Cooperative breeding has recently been documented in 1 female and multiple male groups of the precocial Kalij Pheasant in an introduced population in Hawai'i, where males in the same group cooperatively cared for the young, fought against conspecific intruders and exhibited vigilance against predators. Social groups maintained relatively constant home ranges, and larger groups occupied later home ranges. In 2011, we removed 12 out of 29 groups in the studied population to create vacant breeding habitats. After removal, the subordinate male(s) in 6 out of 10 remaining groups with multiple males left the original groups to establish new groups.

The average number of males in each group decreased from 2.17 (n=29) before removal to 1.36 (n=28) after removal, indicating a decrease in the degree of cooperative breeding in the population. Subsequent to removal, 9 groups contained previously unidentified females, most of which were likely previous floaters. We conclude that habitat saturation contributed to the cooperative breeding in the studied population, while mate limitation is unlikely to be a cause.

Keywords:

Cooperative breeding, Habitat Saturation, Mate Limitation, Removal Experiment, Kalij Pheasant

Introduction

Cooperative breeding occurs when one or more members of a social group provide care to young that are not their own offspring (Stacey and Koenig 1990). It is a relatively rare behavior of particular evolutionary significance because the seemingly altruistic helpers appear to forgo the opportunity to reproduce for themselves, making it a behavior intuitively unstable from an evolutionary standpoint.

Among avian species, cooperative breeding has most often been found and studied in altricial species, in which the helpless hatchlings need extensive care and can receive substantial benefits from helpers (Krebs and Davies 1993). In fact, the reliance of altricial offspring on extensive help from adults is often regarded as a precondition for cooperative breeding in many birds and mammals, in which the increase of reproductive success of the family group often relies on the helpers in some species (Heinsohn 1992; Russell and Rowley 1988). By contrast, cooperative breeding in precocial species is very rare (Cockburn 2006; Du Plessis et al. 1995) and poorly understood. However, it provides an opportunity to examine the influence of extrinsic factors, such as habitat saturation, free from extra-ordinary offspring needs, and fill a major gap in our understanding of the factors influencing cooperative breeding.

Most research has examined the effect of kin selection (Hamilton 1964a; Hamilton 1964b; Maynard Smith 1964) and ecological constraints (Emlen 1982; Emlen 1984) on cooperative breeding. Among ecological constraints, habitat saturation (Brown 1987; Selander 1964) is well supported by empirical studies (e.g., Seychelles warblers *Acrocephalus sechellensis,* Komdeur 1992; Acorn Woodpecker *Melanerpes formicivorus,* Stacey 1979). Breeding habitat is considered saturated when suitable habitats required for successful breeding are fully occupied and surplus young birds can only stay in the natal site (Brown 1987), setting the stage for cooperative breeding behavior to develop. Another commonly considered ecological constraint is mate limitation (e.g., Moustached Warbler *Acrocephalus melanopogon*, Fessl et al. 1996). If there is a shortage of sexually mature individuals of either sex in a population, the lack of a mate (and therefore lack of breeding opportunity) can contribute to individuals of the opposite sex joining breeding groups and providing help to the breeders. In some cases, both habitat limitation and mate limitation attribute to cooperative breeding in a population, such as in the Superb Fairy Wren *Malurus cyaneus* (Pruett-Jones and Lewis 1990).

We recently documented cooperative breeding behavior among male Kalij pheasants *Lophura leucomelanos* in Hawai'i Volcanoes National Park (Chapter 1), which provides an excellent system to examine ecological factors influencing cooperative breeding in a precocial species. In this population, social groups consist of only 1 female with 1 to 5 males, with one male dominant over the others. Two potential reasons may account for the cooperative breeding in this population. First, because the population density was high at the study site, habitat saturation can possibly prevent male offspring from leaving the natal group and establish an independent breeding territory in available habitat. Second, there may be a shortage of females in the population that prevents helpers from breeding independently even if habitat is not saturated. Such ecological limitations can prevent individuals from leaving their natal group and becoming independent breeders (Hatchwell 2007; Krebs and Davies 1993).

We hypothesized that cooperative breeding behavior in this population reflects a shortage of breeding opportunities due to 1) habitat saturation, and/or 2) mate limitation (lack of females). To assess these alternative explanations for cooperative breeding in this population, we experimentally removed some breeding groups from the study area and predicted that when vacant habitats are created, then 1) all sexually mature helpers will remain in their original group if the cooperative breeding is only due to a shortage of females in the population ("mate limitation" hypothesis); 2) sexually mature helpers will disperse and an equivalent number of breeding groups that was originally present will be established in the study area when additional females are available and the reason for cooperative breeding is completely attributed to shortage of habitat ("habitat saturation" hypothesis); or 3) only some sexually mature helpers will disperse and establish new breeding groups with additional females in some of the newly created breeding vacancies, with other vacancies remaining unoccupied (both “habitat saturation” and “mate limitation” hypotheses).

Methods

Study site

The study site is located at the Kipuka Puaulu forest (19°26’ N, 155°18’ W) in Hawai'i Volcanoes National Park (HVNP) on the Island of Hawai'i, USA. It is 42 ha disturbed old growth of native Hawai'ian forest surrounded by relatively recent lava flow fields with scattered shrubs and trees, creating a semi-isolated habitat for the forest-dwelling Kalij Pheasant. Kipuka Puaulu is located around 1200 meters elevation on the southeastern slope of Mauna Loa volcano. In 2011, year-round daily temperature average ranged from 12.5 °C to 25.7 °C, and total precipitation was 129.2 mm (NOAA daily report, http://www.kmc-volcano.com/weather1/daily.htm), within the normal range of local annual rainfall. The trees that formed the forest canopy include 'ohia lehua (*Metrosideros polymorpha*), koa (*Acacia Koa*), manele (*Sapindus saponaria*), olopua (*Nestegis sandwicensis*) and pilo (*Coprosma rhynchocarpa*). The shrub layer was dominated by mamaki (*Pipturus albidus*), and the understory consisted of ferns (such as kupukupu *Nephrolepis exaltata* ssp. *hawaiiensis*), vines (such as Maile *Alyxia stellata*) and invasive grasses (such as meadow ricegrass *Ehrharta stipoides*).

Study species

Kalij Pheasants are native to the western slopes of the Himalayas, where their ecology has not been extensively studied. Their reported mating system includes possible monogamy and polygyny (Ali and Ripley 1969; Barnes 1981; Delacour et al. 1977; Iqbal 1992; Johnsgard 1999; Lewin and Lewin 1984). In 1962, 67 Kalij pheasants were introduced to the Island of Hawai'i from game farms in Texas and Michigan, giving rise to the entire population across various areas of the island later on (Lewin 1971; Swedberg 1967).

HVNP and our field team uniquely metal- and color-banded Kalij Pheasants at the study site, allowing individual recognition by resighting. In January 2011, ~85% of the population were banded, and every social group was recognizable. Kalij Pheasants in the studied population formed stable social groups with cohesive group composition year round and across years (cite Chap1). In 2011, most groups contained 1 female, 1 dominant male, and 0 ~ 4 subordinate males. The only exception was group “O1A”, which only contained 1 old previously dominant male evicted by its previous subordinate group males. This male remained in the area and fought with intruders from other groups even though no female was present in this “group”. Male dominance was stable within social groups. Dominant males were predominantly older than subordinate males with the exception of one group in which the dominant male was the same age as the subordinate male; dominance was not correlated with body measurements (Chapter 1).

All males in a given group grew up in that group, based on pedigree data from our study and Hawai'i Volcanoes National Park (T. K. Pratt, unpubl. data). The group compositions were relatively unchanging, and both sexes were strongly territorial towards their own sex. Cooperative breeding behaviors observed of males in social groups included calling chicks over for food, feeding food items to chicks, exhibiting agonistic behaviors toward conspecific intruders, as well as exhibiting vigilance towards and defending against predators.

The female is likely the dispersing sex in Kalij pheasants, because none of 43 female juveniles banded in the population was resighted after they reach one year old (Pratt and Zeng, unpubl. data), and that female is considered the predominant dispersing sex in birds (Pusey 1987). Although a male-biased adult sex ratio was detected in this population, molecular examination showed that neither the primary sex ratio in eggs nor the secondary sex ratio at hatching differed from 1:1 (Chapter 1), indicating that the male-biased adult sex ratio in residents was likely caused by 2 aspects: 1) on the population level, higher mortality in females, possibly during dispersal; 2) on the group level, male offspring can remain in the group after reaching sexual maturity, while female offspring always disperse.

Population Structure and Social Organization

We conducted population surveys by walking on 30 evenly distributed transects (25 m apart) twice a week throughout the entire study period from January to July 2011. We recorded geographic coordinates and group composition of social groups at each sighting. Every resident social group in the study area was recognizable based on a combination of color bands and individuals with unique morphological characters. We recorded sightings of resident groups with established home ranges, as well as that of floater males and females (non-group affiliated individuals without an established home range). We recorded the geographic coordinates of each sighting using a Garmin eTrex Legend HCx Geographic Positioning System (Schaffhausen, Switzerland).

Removal experiment

In 2011, we conducted a removal experiment in a core area of ~27 ha within Kipuka Puaulu in order to test the effect of habitat saturation on cooperative breeding in this population. At the time, 85% (57M, 20F) of the 91 resident individuals in the core area were uniquely metal and color-banded, allowing individual identification by resighting (Chapter 1).

From February 21 to March 6, 2011, before the breeding season (from April to July, Chapter 1) started, we removed ~40% of the groups (12 out of 29 groups, including 23 males and 11 females) in the core area to create vacant habitats available to individuals in remaining groups, as well as floaters. We selected groups to remove using a stratified randomization technique (Kenkel et al. 1989). We first stratified all groups into 5 categories based the number of male members, and then randomly chose about a third of the groups in each category to be removed. We mapped the home ranges of all breeding groups from January 13 to February 21, 2011, and re-randomized chosen groups when spatial clumping was detected on the home range map, until reaching a relatively even overall spatial distribution. Among the 12 groups removed, 5 consisted of 1 female and 1 male, 3 consisted of 1 female and 2 males, 1 consisted of 1 female and 3 males, 2 consisted of 1 female and 4 males, and 1 only consisted 1 male (group "O1A"). We translocated removed pheasants to the Kahuku unit of HVNP ~110 km away from the study site.

We recorded and measured group size, group composition, total number of groups, home range sizes and geographic coordinates of sightings before the removal (from January 13 to February 21, 2011) as well as three weeks after removal, after new group composition and home ranges were relatively stabilized (from March 25 to July 1, 2011).

To examine the effect of removal experiment on population structure and group composition, we compared population structure and group composition before and after removal. Since the change of group composition before and after removal might not be attributed to the experimental effect, but rather to a natural change in the timing of the spring breeding season every year, we also compared the data with that of the same period (from February to July) in 2010, to exclude this possibility.

We carried out fieldwork that included capturing, banding, removal and relocation of the Kalij pheasants under the Protected Wildlife Permit No. WL010-06 (Department of Land & Natural Resources, State of Hawai'i, USA), Scientific Research and Collecting Permit No. HAVO-2010-SCI-0025 (National Park Service, U. S. Department of the Interior), as well as Animal Care and Use Protocol No. A-20080047 (the University of California, Riverside).

Home range analysis

We calculated home ranges using sighting data that included information on date, time and geographic coordinates. We recorded sightings at least 5 minutes apart, collected no more than 3 sightings of the same group at each encounter, and collected no more than 5 sightings each day. Because group members predominantly move together, we used the coordinates of the dominant male to calculate the home range for each group.

We used the Home Range Tools package (HRT) in ArcMap 9.3 software (ESRI, Inc. 2008, Redlands, USA) to perform Fixed Kernel analysis on home ranges for social groups. To select a suitable smoothing parameter, we used the h_{ref} value of 30 that was suggested by HRT as the square root of the mean variance in x (var_x) and y (var_y) co-ordinates divided by the sixth root of the number of points (equation [1], (Worton 1995)).

$$h_{ref} = n^{-1/6}\sqrt{\frac{var_x + \mathrm{var}_y}{2}} \quad [1]$$

We used a raster cell size of 5 × 5 m^2 and a scaling factor of 1 000 000, which were suitable for the scale and distribution of the sighting data, and set the isopleth to 80% to create the polygons. Polygon shape and size were output from each Fixed Kernel analysis.

To determine the minimum number of sightings required for valid home range analysis, we selected 3 individuals with more than 50 sightings and with relatively small, medium and large home ranges, respectively, for preliminary analysis. For each individual, we randomly chose sets of 3, 5, 7… 49 sighting points to calculate home range areas using the above parameters, repeating 10 times for each set. We plotted all results for each individual to fit a logistic curve and detected the asymptotes. Then we calculated the 95% value for each asymptote, and the largest number of sighting points needed to reach this value among the 3 individuals was 19.3. Therefore, we only used groups with 20 or more sightings in home range analyses.

To illustrate the dynamics of group turnover after the removal experiment, we used the utilization distribution overlap index (UDOI, Fieberg and Kochanny 2005) to estimate the degree of overlap between home ranges. UDOI value increases with the degree of overlap. We calculated UDOI in Program R 3.0.1 (R Development Core Team 2013) using the adehabitat package (Calenge 2006). To investigate the difference of different males' tendency (dominant vs. subordinate) of staying at the original home range after removal, we calculated the UDOI of each male's home range after removal to his original home range before removal, and compared those overlaps of dominant males to those of subordinate ones. We used a linear mixed model with the overlap index as response variable and male identity as explanatory variable. We included group identity as a random factor to account for the non-independence of subordinate males of the same original group.

Results

Background

No detailed observation on reproductive success and its effect on population demography was available prior to 2009, but we identified 5 male juveniles in the population in 2009, indicating some reproductive success in 2008. Reproductive success was high in 2009, resulting in 46 juveniles (27M, 19F) and a relatively large resident number in the population in 2010. In contrast, reproduction in 2010 appeared very low, resulting in 0 juveniles and a relatively small resident number in 2011.

Sighting data from 2010 indicated that there were 30 social groups and a total of 120 resident Kalij Pheasants (72M, 48F) in the population in February 2010 before breeding season started. From February to June 2010, 3 males and 19 females disappeared, possibly due to dispersal. Two of those males and all 19 females were juvenile offspring hatched in the previous year, and 1 male was an adult age 3 years or more. One adult solo female (age 9 years old or more) and 1 adult male (age 10 years old or more) disappeared most likely due to mortality. By July, there remained 29 social groups and a total of 97 resident individuals left. No group division was recorded.

Population structure and group composition before and after removal

The population survey documented and monitored all resident individuals in the 27-ha core area. After the 12 groups (23M, 11F) were removed (out of 29 original groups) to create vacant breeding habitats, 6 groups fissioned into 14 new groups, and 3 new groups came in, resulting in a total of 28 new groups (Table 2.1).

Table 2.1. Population structure before and after removal.

	# Resident M	# Resident F	Residents/ha	Adult Sex Ratio (M/F)	# 1M groups	# ≥2M groups
Before removal	63	28	3.37	2.25	12	17
Removed	23	11	1.26	2.09	6	6
After removal	38	24	2.30	1.58	20	8

In the 29 old social groups before removal, 28 contained 1 female, and 1 to 5 males (2.14 ± 1.30, n=29), with one male being dominant, and 1 group (group "O1A") only had 1 male with no female.

A total of 15 out of 22 previously subordinate males moved out of their original social groups after the removal, and the proportion of multiple-male groups dropped significantly after removal (Fisher's Exact test P=0.033; Figure 2.1).

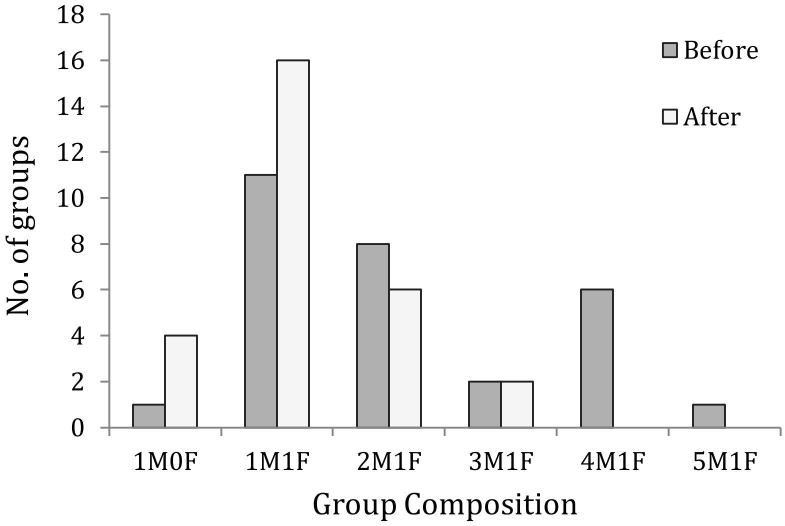


Figure 2.1. Social group composition before and after removal. The average number of males in each group was 2.17 among the 29 groups before removal, and 1.36 among the 28 groups after removal.

Among the 28 groups (38M, 24F) after removal, most groups (25) contained males from original resident groups; the 3 exceptions contained previously unidentified males that were either residents outside of the core area or floaters prior to the experiment. In the 25 post-removal groups that contained males in original groups, 8 had unchanged composition (both males and females), 8 contained previously dominant males (with or without some previously subordinate males), and 9 contained previously subordinate males (with no previously dominant males).

Sixteen of 17 females from original groups remained in the population after the removal experiment, and one previously unbanded female disappeared. Aside from the 8 groups with unchanged composition, 6 females stayed with the previously dominant males in fissioned groups, 2 females switched groups from 2 original groups containing 1M1F to 2 previously subordinate brother pairs that left their original groups, and left their previous mate single after removal. The other 8 females in newly established groups were previously unidentified and were most likely floaters prior to the experiment (Figure 2.2).

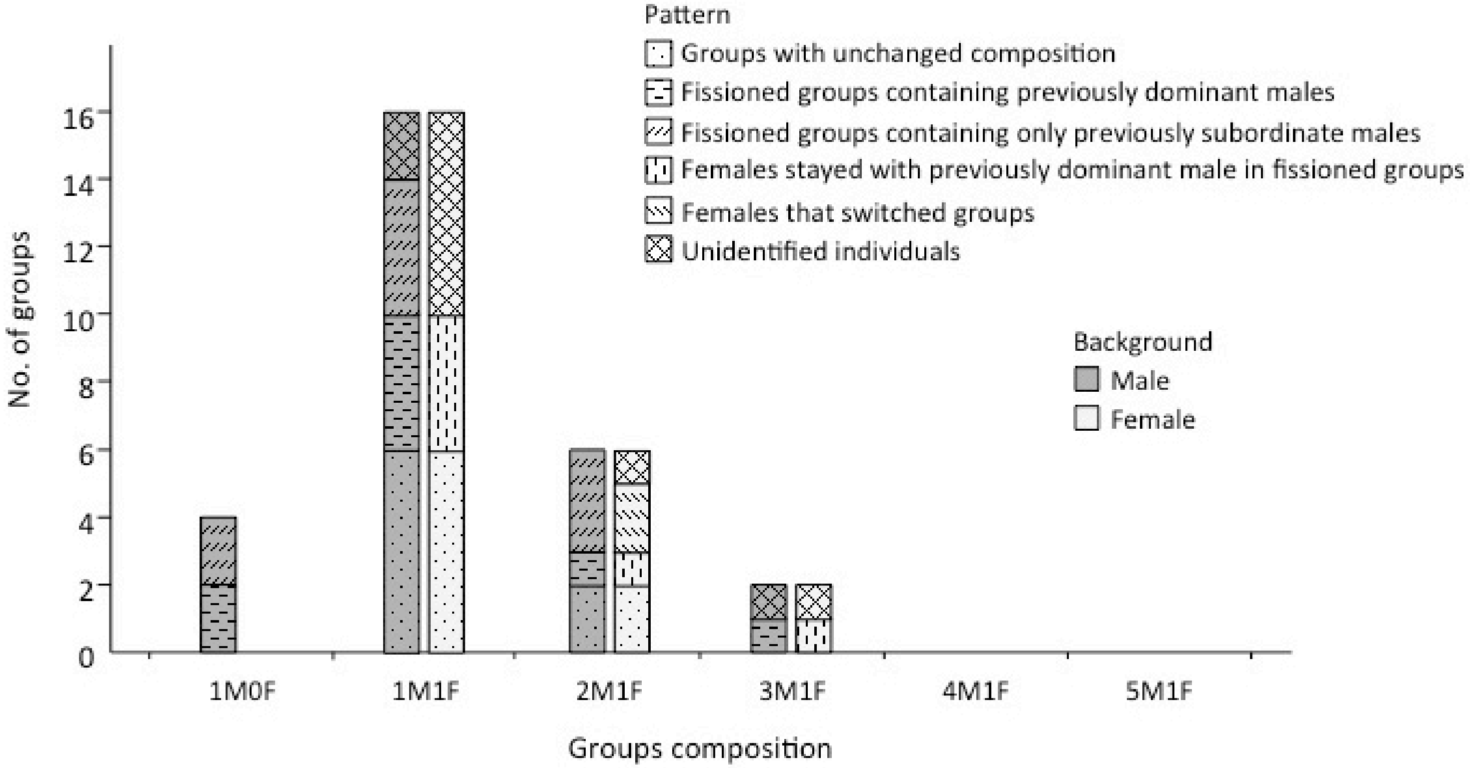
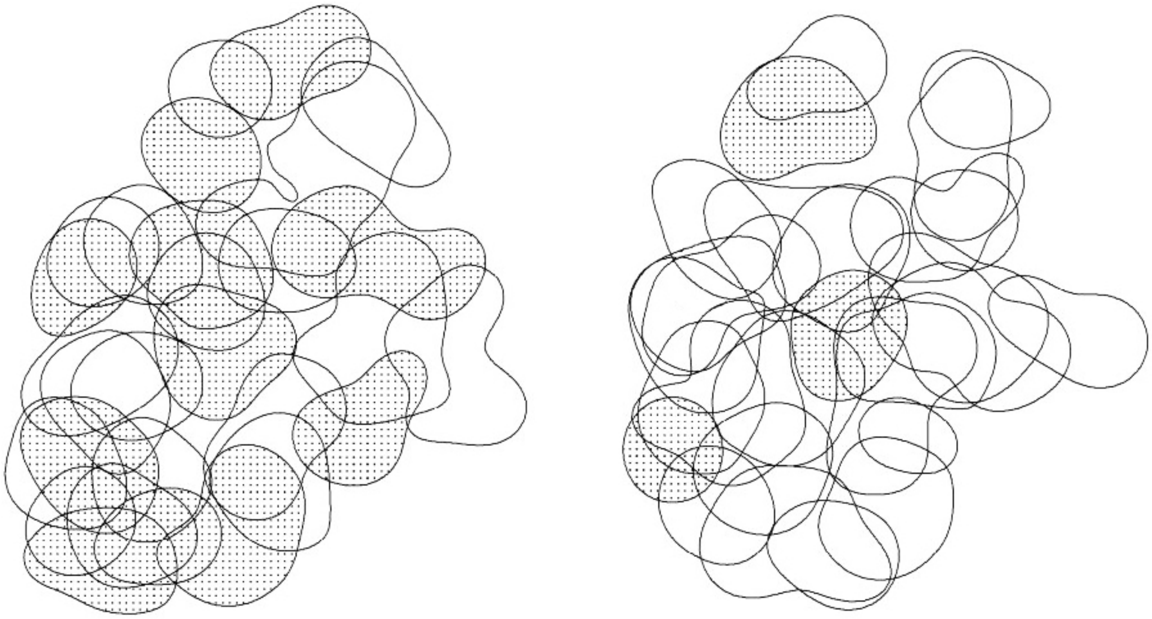


Figure 2.2. Sources of group members after removal. Approximately two thirds of males in post-removal 1M groups were members of previous multiple-male groups. Most females from original groups stayed with the dominant male of the original group after removal.

Home range size and overlap

Each group maintained a home range, which overlapped with neighbors from all sides both before and after removal. The home range size of social groups was $\bar{x} \pm SD =$ 2.04 ± 0.56 ha (n=22) before the removal experiment, and 2.30 ± 0.80 ha (n=20) afterward. There was not a significant difference in home range size before and after removal (*t*-test, p=0.216) (Figure 2.3).



Home ranges before removal
Jan. 13th – Feb. 21st 2011

Home ranges after removal
Mar. 25th – Jul. 1st 2011

Figure 2.3. Home range of groups before and after removal. Shaded home ranges in before-removal map represent removed groups; shaded home ranges in after-removal map indicate subsequent groups that did not contain members from original groups. Groups lacking sufficient sighting data were not included in home range analyses, but are presented here.

Among original groups prior to removal, home-range size increased with the number of males in the group (Spearman's rank correlation, df = 20, r_s=0.546, t=2.91, p = 0.008. Figure 2.4).

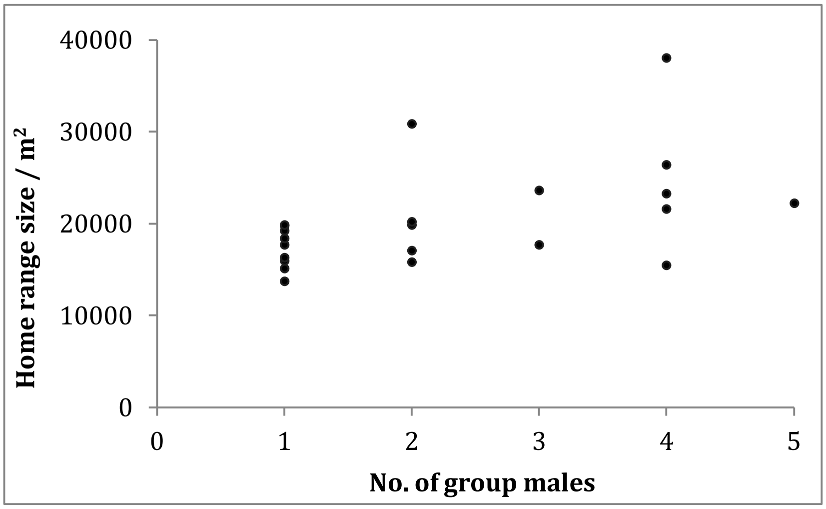


Figure 2.4. Home range size in relation to number of males in the same social group.

Among the 6 original groups with multiple males that fissioned, we were able to calculate home ranges for the original group and all subsequent groups for 4 of them (Table 2.2). The UDOI between the subsequent groups and original groups showed that dominant individuals stayed nearer their previous home-range, whereas subordinates moved further (linear mixed model, $F_{1,7}$ = 86.5, p < 0.001). The same trend was detected for the 2 other groups that fissioned; however, we do not have sufficient sighting data to calculate home range for all groups that arose from these two.

Table 2.2. The utilization distribution overlap index (UDOI) of an individual male's post-removal group's home range with his pre-removal group's home range depending on his dominance status prior to removal. Note that the UDOI value increases with the degree of overlap.

Original group	Previous dominance status of males in fissioned groups		
	Dominant	Subordinate-1	Subordinate-2
1A	0.590	0.072	
Deadbeats	0.442	0.152	0.216
South Side 2	0.523	0.121	
Whites	0.479	0.079	

Discussion

Kalij Pheasants in this population formed social groups between one female and one to multiple males, with larger groups occupying larger home ranges. Our removal experiment resulted in a decrease in the number as well as proportion of cooperative groups, suggesting habitat saturation was an attributive factor for cooperative breeding in this population. On the contrary, female limitation was not a crucial factor causing the cooperative breeding.

The experimental results were unlikely products of natural changes of group composition happening during the season when the experiment was conducted. This is because during the same period (from February to July) in 2010, without the interference of the removal experiment, no group turnover (in terms of group division and the establishment or disappearance of groups) was recorded.

Due to high reproductive success in the population in 2009, the number of juveniles in 2010 (28M 19F) and the number of 2-year old males in 2011 (25M) was high. In 2010, reproductive success was low and no juveniles were recorded in the population in 2011. It is not clear how this influenced the group division after our removal experiment in 2011. However, long-term monitoring by the United States Geological Surveys Pacific Research Center in Hawai'i Volcanoes National Park fro 2003 to 2009 (T. K. Pratt, unpubl. data) has never observed large-scale group turnover within a year. This suggests that the possibility of high reproductive success in 2009 influencing group division after removal is low. Moreover, 5 subordinates in 5 different groups near the periphery of the core area disappeared after the removal experiment. They might have died, established home range outside of the core area, or became floaters, and were not included in group composition or population structure statistics after removal.

Effect of group size on home range size

Before the removal experiment, original groups with more males occupied larger areas of home range, suggesting that cooperation among males can lead to larger share of resources (at least as measured by home range size) of the group in the population. Similar trend was found in other cooperatively breeding species such as Green Woodhoopoes *Phoeniculus purpureus* (Ligon and Ligon 1990) and Galápagos

Mockingbirds *Mimus parvulus* (Curry and Grant 1990). As with these two species, all group members in the study population of Kalij Pheasants participated in vigorous agnostic behavior against other groups when encountered; presumably, more participating individuals offer greater advantages in territory defense, and likely contribute to larger territories.

Effect of mate limitation

Our results suggest that cooperative breeding by subordinate males was unlikely attributable to lack of mates. First, we recorded floater males and females during surveys, and previously subordinate males were able to quickly form new groups with previously non-group-affiliated females. Second, in one group, we were only able to remove the males but not the female at the first attempt. The remaining female had acquired an unidentified male in her home range two days later when we succeeded in removing the female but did not remove the new male. This new male stayed in that home range and acquired a previously unidentified female after one day. The above suggests that mate limitation was not a crucial limiting factor that caused cooperative breeding in this population.

Interestingly, two males from previously 1M1F groups who lost their mates to 2 pairs of brothers that had been subordinate males in original groups did not acquire new mates after removal. This suggests that availability of female mates was a limiting factor that prevented males from independent breeding in some cases, possibly after the majority of previous floater females had joined new groups in available habitats. However, in 2 new groups subordinate males left their original groups without acquiring a female subsequent to leaving, suggesting that mate limitation was not the limiting factor that prevented subordinate males from leaving the family group, and further supporting habitat saturation as being the principal contributing factor to cooperative breeding in this population.

Effect of habitat saturation

Our removal experiment supported the hypothesis that habitat saturation may contribute to the cooperative breeding behavior of Kalij Pheasants in this population. First, we found a significant decline in the number and proportion of multiple-male groups after the removal experiment. Approximately two-thirds of previously subordinate males left their original groups and established new home ranges at the study site. Second, the number of groups with established home ranges was similar before and after removal, suggesting that mate limitation may not be a major reason constraining subordinate males from establishing independent groups in this species. These results were consistent with the predictions of the “habitat saturation hypothesis”, implying that habitat saturation played a possible role in the cooperative breeding behaviors of Kalij Pheasants. Available literature indicates a 10-fold lower population density of Kalij Pheasant and their closely related species in their natural habitat in the Himalayas (Chapter 1), suggesting the Kalij Pheasant density at our study site was extremely high. Given that the total number of groups with established home ranges was similar before and after removal, environmental carrying capacity for groups was likely reached both before and after the removal experiment. This was also reflected by the fact that the home range size did not change significantly before and after removal, strongly suggesting that the observed home range size is required to provide adequate resources to support a breeding group.

Interestingly, among the 6 multiple-male groups that fissioned after the removal experiment, dominant males overlapped most with their previous home range whereas subordinate males shifted to a peripheral area in relation to the previously dominant male. This might suggest that dominant males had a preference for the original home range, and imply the dynamics that when empty habitat was created (naturally or artificially) and pressure for delaying dispersal was relieved, subordinate males tend to disperse from the original group and establish independent breeding habitats on their own.

Heterogeneity in habitat quality can also play an important role in the formation and distribution of cooperative breeding in a population. For instance, offspring in higher-quality habitats can gain higher lifetime-fitness by delaying dispersal and breeding at the natal site later as compared to breeding in lower-quality habitats even if they are currently available (Koenig et al. 1992; Komdeur 1992). In this population, whether cooperative breeding occurred only in higher-quality habitats on the group scale within the kipuka is unclear due to lack of data on habitat quality. However, on the population scale, male offspring staying within the forested kipuka presumably can gain future reproductive opportunities when they become the oldest of the group (Chapter 1), thereby maintaining access to better ecological resources rather than dispersing to the relatively barren lava fields outside of the kipuka. Therefore the difference in habitat quality between areas within and outside of the kipuka may have contributed to the formation of cooperative breeding in this population.

A common challenge to the importance of habitat saturation in influencing cooperative breeding is that ecological constraints are ubiquitous in nature (Heinsohn et al. 1990) while cooperative breeding is not. Although this study demonstrated the direct influence of habitat saturation on the formation of cooperative breeding in this population, habitat saturation alone usually does not entirely explain the delayed dispersal of offspring and subsequent cooperative breeding (Koenig et al. 1992; Smith 1990). In fact, cooperative breeding is unlikely the result of any single factor. To better understand the great diversity in the forms of cooperative breeding in birds demonstrated by various studies, cooperative breeding can be viewed as the consequence of a complex combination of factors including but not limited to certain life history traits that predispose delayed dispersal such as high longevity and low annual adult mortality (Arnold and Owens 1998); survival rate of “surplus individuals” in comparison to that of breeders (Brown 1987); ecological constraints (Emlen 1982; Emlen 1984), including habitat saturation and mate or food limitation (such as food availability in the Pied Kingfisher *Ceryle rudis*, Reyer 1990); peculiar life history traits such as cavity roosting of the Green Woodhoopoe *Phoeniculus purpureus* (Ligon and Ligon 1990) that promote cooperative breeding. Moreover, the evolutionary trajectories of cooperative system may be diverse among cooperative breeding lineages (Cockburn 2013) in which founding conditions for cooperative breeding could have sometimes changed and become hard to identify with the present condition.

At our study site, the forested kipuka represent high quality habitat containing resources such as food, cover, roosting sites and breeding sites; in contrast, quality of the large area of sparsely forested lava fields around the kipuka was low, imposing increased difficulty for survival and breeding. On the other hand, suitability for floaters may be low, because resident density was high, and floaters were always chased away by residents. Therefore, group affiliation in the kipuka may offer great advantages attributable to subordinate males staying in the social group instead of dispersing, and subsequently cooperatively breed.

To conclude, our results demonstrate that Kalij Pheasants exhibited cooperative social behaviors in response to ecological factors, and suggest that habitat saturation may be the principal reason for the patterns of social behavior and cooperative breeding we observed. To our knowledge, our study is among the few in the literature that provides experimental evidence for the role of habitat saturation on social behaviors and cooperative breeding in birds.

In Kalij Pheasants, the precocial chicks do not require as intensive parental care as observed in altricial species, in which cooperative breeding is most commonly found. Therefore, it demonstrates that vigorous offspring demand is not a necessary precursor of cooperative breeding, and makes a strong case how ecological factors, particularly habitat saturation in this case, directly influenced cooperative breeding in a behaviorally plastic population.

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Chapter 3: Genetic Evidence of Complex Reproductive Strategies and Social Structure in a Recently Established Bird on the Island of Hawai'i, the Kalij Pheasant (*Lophura leucomelanos*)

Abstract

Genetic-based analytical approaches have revolutionized our understanding of mating strategies and social behaviors in birds in recent decades. In cooperatively breeding species, unbiased characterization of the genetic mating system and relationship among social unit members can help illustrate the benefits and costs of social behaviors. Cooperative breeding was recently reported in the precocial Kalij Pheasants (*Lophura leucomelanos*) in Hawai'i, where social groups sometimes included one female with multiple males with one male dominant over the other(s). The genetic mating system and relatedness among group members are not known. Using 88 adult samples, 82 egg samples and 12 autosomal microsatellites, we applied genetic analyses to reconstruct relatedness patterns within groups and the genetic mating system in this population. We analyzed relatedness for 32 within-group dominant-subordinate male dyads from 17 groups, using program CERVUS 2.0. 34.4% of the dyads were related, indicating these helpers can gain indirect fitness by helping kin. We analyzed parentage for 82 offspring from 13 broods using program ML-RELATE. Three offspring were likely conspecific brood parasites. 68.4% of the remaining 79 offspring were fathered by the dominant male of the social group, while 16.5% were fathered by the subordinate males of the group, suggesting that helpers gained some direct benefit by sharing reproduction. In addition, benefits of group-living may have also contributed to the cooperative breeding of Kalij Pheasants in this population.

Keywords:

Pheasant, cooperative breeding, genetic mating system, relatedness, dominance

Introduction

Mating systems, the mate-obtaining strategies of a species or population, are fundamental traits in animals' social life (Emlen and Oring 1977). Birds offer excellent opportunities to investigate mating systems and their evolutionary maintenance because avian mating systems show substantial inter- and intra-specific variations (Reynolds 1996). Although social monogamy was traditionally considered the most prevalent type of avian mating system, a growing number of genetic studies have demonstrated that the exclusively monogamous mating relationship between a male and a female is actually less frequent in nature than previously thought (Griffith et al. 2002). Indeed, genetic-based parentage and relatedness analyses and the rapid development of high-resolution genetic markers, i.e., microsatellites and single nucleotide polymorphisms (Weir et al. 2006), as well as sophisticated analytical approaches (Jones and Ardren 2003), have revolutionized our understanding of avian mating systems in the last few decades.

Genetic-based studies have revealed previously less well recognized mating system features such as extra-pair paternity (EPP) (e.g., Westneat 1987) and conspecific brood parasitism (CBP) (Andersson and Åhlund 2000). In contradistinction to the observation-based traditional view that most avian species breed monogamously (Lack 1968), genetic-based research have shown that EPP is a prevalent alternative reproductive strategy in birds, occurring in 86% of species reviewed by (Griffith et al. 2002). Current explanations for EPP include females seeking to guard against infertility in their social mates (Wetton and Parkin 1991; Sheldon 1994), to maximize genetic benefit for offspring (Westneat 1990; Birkhead and Moller 1992; Tregenza and Wedell 2000), and to obtain nongenetic resources (Burke 1989; Colwell and Oring 1989). CBP has been reported in at least 234 avian species, occurring predominantly in precocial and semipreciocial avian taxa such as the Galliformes (pheasants, partridges and grouses) and Anseriformes (ducks and geese) (Yom-Tov 2001). This uneven distribution may be explained by the fact that precocial species generally lay larger clutches than do similarly sized altricial species (Ar and Yomtov 1978) and typically start incubating and guarding the nest after reaching full clutch size (Yom-Tov 2001); in addition, parasitic offspring require less parental care than altricial species (Sorenson 1992). However, more detailed genetic studies are needed for comparative analyses and a better understanding of how proposed factors contribute to such traits.

In cooperatively breeding species, individuals can become helpers when the benefit of helping other individuals in a group outweighs that of breeding itself (Hatchwell and Komdeur 2000). The benefits and costs of social behaviors are complex, and unbiased characterization of a genetic mating system and the relationship among social unit members can help illustrate such costs and benefits from evolutionary perspectives. Hamilton (1964) and Maynard Smith (1964) proposed the hypothesis of kin selection based on the theoretical framework of inclusive fitness, which suggests that a helper's indirect fitness increases with the reproductive success of collateral kin. From this perspective, cooperation can be viewed as an adaptive consequence of its effect on the inclusive fitness of the helper and its genetic relatives, and therefore favored by natural selection (Komdeur 1994; Hatchwell et al. 2001; Griffin and West 2002). Kin selection is widely accepted as a contributing factor in the evolution of cooperative breeding (Brown 1987; Emlen and Wrege 1988; Cockburn 1998; Clutton-Brock 2002). For instance, it helps to explain offspring from previous broods that delayed dispersing due to ecological constraints may stay in the natal group and help rearing younger siblings (Ekman et al. 2004).

Alternatively, helpers may gain direct benefits that enhance their own reproductive success (Richardson et al. 2001), which helps to maintain cooperative breeding in a population. For instance, helpers can be genetically unrelated to the breeders and gain some level of parentage of the offspring they help caring for (Clutton-Brock et al. 2001; Richardson et al. 2002). In fact, many earlier studies suggest that subordinate males are more prone to help if they share paternity of offspring (Magrath and Whittingham 1997; Whittingham et al. 1997). In reality, the pattern of social organization of cooperative breeders can be rather complicated, with the possibility of having both kin-based and unrelated individuals in a social group (Hatchwell 2009; Preston et al. 2013). To understand the functional significance and evolutionary drivers of cooperative breeding, it is necessary to examine the relatedness among individuals in social groups (i.e., the genetic social structure), and to determine how reproduction is shared among individuals (Hatchwell et al. 2002).

Cooperative breeding was recently documented in Kalij Pheasants (*Lophura leucomelanos*) that were introduced to the island of Hawai'i (Chapter 1), a behavior which has not been noted in other accounts of the ecology of this species in their native range (Ali and Ripley 1969; Delacour 1977; Iqbal 1992; Johnsgard 1999). Previous field research at our study site (Chapter 1) indicated that one female and 1 to 6 males usually formed a stable social group with one male dominant over the others. Group members predominantly stay together in a constant home range. Most males with a clear pedigree grew up in the social group after color-banding, and may be related to each other. Cooperative breeding behavior, including caring for chicks, was observed among all adults. Courtship-displays to the group female were observed from subordinate males and males from other groups, although dominant males were always observed to intervene. Mating events were not observed.

Based on the above field observations, we hypothesized that 1) kin selection contributed to the formation of cooperation among closely related individuals, and predicted that the relatedness among group males was high; 2) helpers gained direct benefit through reproductive share, and therefore we predicted that subordinate males unrelated to the group female sired a proportion of the offspring from the social group.

Here, we used multi-locus autosomal microsatellite analyses to determine the mating system and resolve the social structure and reproductive share in this population of Kalij Pheasants, and attempted to demonstrate contributing factors underlying their possibly recently arisen cooperative breeding behavior in a new environment. Previous studies have obtained patterns of group organization and apparent social structure from field data (Chapter 1, Chapter 2). To extend these results, here we analyzed the mating system based on genetic relationships between males, females, and chicks. In particular, we applied genetic relatedness and parentage analyses to determine: (1) the relatedness of subordinate males (helpers) to dominant male and female of the social group; (2) reproductive share among group males; and (3) whether alternative reproductive strategies, i.e., extra group paternity and conspecific brood parasitism, exist in this Hawai'ian population of Kalij Pheasants. Insights into these questions can help us better understand the basis for the evolutionary maintenance of social behaviors such as cooperative breeding in Kalij Pheasants.

Materials and methods

Study site and the study species

This study took place in the 40-ha Kipuka Puaulu forest (19°26’ N, 155°18’ W, 1,100 meters a.s.l.) in Hawai'i Volcanoes National Park on the Island of Hawai'i, USA. Such habitat is semi-isolated for the forest-dwelling Kalij Pheasant, as the forest is surrounded by relatively recent lava flows with sparse shrub and tree cover. The mean annual temperature is around 16°C, with a difference of about 3.5°C between the hottest and coolest months. Annual rainfall is approximately 1500 mm, with a relatively wet summer and dry winter (Mueller-Dombois and Lamoureu 1967).

Kalij Pheasants are native to South Asia (del Hoyo et al. 1994). Limited field observations in their native range suggested that the mating system of this species can be socially monogamous or polygynous (Ali and Ripley 1969; Delacour 1977; Iqbal 1992; Johnsgard 1999). However, no genetic-based study up to now has attempted to explore mating system variation in this species. Kalij Pheasants were introduced to the Island of Hawai'i in 1962, when 67 individuals were transported from game farms in Texas and Michigan; these 67 birds are believed to be the sole source of the abundant island population observed subsequently (Lewin 1971; Lewin and Lewin 1984). In our study population, social groups were stable and usually included one female with multiple males. Each group stayed in a relatively constant home range, which overlaps with the home range of neighboring groups. Group members predominantly stayed and moved together. Only in rare cases were individuals observed to move considerable distances outside the home range. Cooperative social behaviors exhibited by all adults in a group included caring for chicks, such as food provisioning, cooperative defense against conspecific intruders, and vigilance against predators.

Sample collection and DNA extraction

We collected 170 genetic samples of Kalij Pheasants at the study site, including 88 adults (60 males and 28 females) with known group affiliation who lived in the population from 2009 to 2011, with samples collected between 2003 and 2011, and 82 offspring samples collected from 13 nests between 2009 and 2011. Nine of 13 nests were sampled completely, while 4 nests were sampled incompletely due to nest predation or sample degradation at the time of collection. For adults, we took approximately 100 μl blood from the brachial vein of each individual. For offspring, we collected the egg membrane containing visible blood vessels inside the freshly hatched egg of each individual. Both types of samples were preserved in 99.5 % Ethanol at −20 ˚C. Total genomic DNA was extracted using DNA extraction kit DP318 (TianGen Biotech, Beijing, China). The resulting DNA samples were quantified using NanoVue Plus spectrophotometer (GE Healthcare Bio-Sciences, Pittsburgh, USA), standardized to a concentration of 50 ng/μL, and then stored at -20°C for further microsatellite genotyping. Capturing, ringing and sampling of blood or egg membranes from Kalij Pheasants were carried out under Department of Land & Natural Resources (State of Hawai'i, USA) Protected Wildlife Permit No. WL010-06, National Park Service (U. S. Department of the Interior) Scientific Research and Collecting Permit No. HAVO-2010-SCI-0025, and University of California, Riverside, Animal Care and Use Protocol A-20080047.

Microsatellite genotyping

We screened a subset of DNA samples with 89 microsatellite markers originally developed for related pheasant species from published sources (Hennache et al. 2003; Wang et al. 2009a; Wang et al. 2009b; Dong et al. 2013) and unpublished markers from MOE Key Laboratory for Biodiversity Science and Ecological Engineering, Beijing Normal University. We used the strategy described by Gu et al. (2012) to check the amplification success and polymorphism of these candidate microsatellites, and linkage disequilibrium analysis to exclude linked loci. All these efforts eventually led to a final panel of 12 autosomal microsatellite loci for this study (for characters and references, see Supporting Information Table S3.1. The forward primers were labeled with one of three fluorescent dyes (FAM, HEX or ROX; Applied Biosystems) at the 5’ end, and most of the reverse primers were modified by placing a ‘pig-tail’ extension (GTTTCTT) at the 5’ end to facilitate accurate genotyping (Brownstein et al. 1996). We arranged these 12 primer pairs into 7 multiplex sets for PCR amplifications (Table S3.1). All Multiplex PCR reactions were prepared using the QIAGEN Multiplex PCR Kit (QIAGEN, Hilden, Germany). PCR amplification was carried out in a 10 µl reaction volume using 5 µl Multiplex PCR Master Mix, 1 µl primer Mix, 3µl RNASE free water and 1 µl DNA sample. The PCRs were performed on thermal cyclers (Applied Biosystem® GeneAmp 2700) with the following conditions: 15 min at 95°C, 35 cycles consisting of 30 sec at 94°C, 3 min at 57°C, and 1 min at 72°C, followed by a final 15 min extension step at 72°C. PCR products were separated by capillary electrophoresis on an ABI 3700 Genetic Analyzer (Applied Biosystems). Fragment length was assigned using an internal size standard (GeneScan™-500LIZ®, Applied Biosystems) and visualized using GeneMapper® software v.3.7 (Applied Biosystems). All offspring egg membrane blood and 20% of randomly chosen adult brachial vain blood samples were genotyped twice independently to ensure genotyping repeatability (Gu et al. 2012; Gu et al. 2013) .

Population genetic analysis

Because the microsatellite loci used in this study were originally isolated from other pheasant species, a relative high rate of PCR failure due to cross-species amplification may increase the presence of null alleles (Selkoe and Toonen 2006), which may be a problem for further statistical analyses. We tested the allelic dropout, stuttering, and false alleles using Micro Checker v2.2.3 (Van Oosterhout et al. 2004) and estimated null allele frequencies for each locus using the EM algorithm with the program FreeNA (Chapuis and Estoup 2007). We tested deviations from Hardy–Weinberg equilibrium, genotypic equilibrium, and the inbreeding index F_{IS} for each locus of the study population, and we assessed its significance based on 1 000 permutations with program CERVUS v.2.0. The same program was used to calculate the number of alleles (N_A), and observed (H_O) and expected heterozygosities (H_E) in each population location. We corrected the nominal significance level of $P = 0.05$ for multiple testing using the sequential Bonferroni procedure (Rice 1989).

Relatedness analysis

To explore the pattern of relatedness among adult Kalij Pheasants, we calculated the pairwise relatedness coefficients (R) among all possible pairs of individuals (referring to any combination of two individuals of interest, hereafter “dyads”). The R value ranges from -1 to 1 and measures the degree of relationships between individuals, which is defined as the proportion of ancestral alleles that are shared between two individuals (Lynch and Walsh 1998). This approach allows a multi-locus estimation using polymorphic microsatellites (Liu et al. 2013). The larger the R value is, the closer the relationship between two individuals; negative R values can be interpreted as indicating that the two individuals are less related than two random individuals from the focal population (Hardy 2003).

We conducted relatedness analyzes using the program ML-RELATE (Kalinowski et al. 2006) in order to calculate maximum likelihood estimates of relatedness and the likelihood of four relatedness categories (unrelated: R = 0; close kin e.g. half-siblings, uncle-nephew: R = 0.25; full-siblings: R = 0.5; parent–offspring: R = 0.5), and to determine the proportion of a specific relatedness category among all pairwise comparisons between adult Kalij Pheasants. For all relatedness estimation, we applied the Queller and Goodnight estimator (Queller and Goodnight 1989), a widely used relatedness estimator to calculate pairwise relatedness coefficients.

We further carried out a rarefaction analysis based on the full dataset and a subset of data with only adults, using the web-based program RE-RAT (Schwacke et al. 2005) in order to determine the number of microsatellite loci that enables stable relatedness estimation. In particular, this method helps to calculate relatedness coefficients under a given number of available loci.

Parentage analysis

We assigned parentage to offspring using the program CERVUS v.2.0. Because dominant males were observed to prevent other males from courting the group female (Chapter 1), we defined the putative mother as the group female and putative father as the dominant male of the group. First, we compared the number of microsatellite mismatches between offspring and the putative mother to the average number of mismatches between randomly paired offspring and females sampled from the population to help detect any instances of conspecific brood parasitism. Offspring not sired by the putative mother were considered conspecific brood parasites, and were not included in paternity analysis. Second, we analyzed the likelihood of offspring parentage given the genotype of the population using multi-locus genotypes in CERVUS. Adult allele frequencies were calculated to ensure that all markers met Hardy-Weinberg equilibrium. Then we ran a simulation of parentage analysis to calculate the confidence of parentage assignments and ensure that the data and analyses were suitable for unbiased estimation. A paternity analysis setting the group female as known mother was then done to all offspring, outputting all father candidates in the population with a positive trio-LOD (logarithm of odds) value. LOD value suggests that the putative parent is more likely to be the true parent than not the true parent, and such likelihood increases with LOD value. Paternity was assigned to the candidate father with the highest trio-LOD value, excluding combinations that were impossible in time (candidate fathers unborn or disappeared at the time) or space (if there was one or more home ranges between the home range of the candidate father and that of the target family, because individuals were rarely observed to travel this far, Chapter 1).

Results

Population genetics characteristics

All of the 170 individual samples of Kalij Pheasants were successfully amplified at seven loci. For the remaining five loci, the success rate varied between 97.1% and 99.5% (Table 3.1). We found no evidence of genotyping error of stuttering or large-allele drop-out, but the presence of null alleles at all loci was suggested by Micro Checker. The null allele frequencies were low across all loci (0 ~ 4.72%, mean ± S.D. = 1.45% ± 1.40%) as estimated by FreeNA. This level of null allele can be negligible for parentage analysis based on a simulation study (Dakin and Avise 2004). The 12 microsatellites loci had 2-5 alleles (3.00 ± 1.04) per locus. The genetic diversity varied across loci (observed heterozygosity: 0.33-0.69). No significant heterozygote deficits were observed at the loci, but 6 loci had a positive F_{IS} value (Table 3.1). Moreover, we found that 4 of 66 pairs (6.06%) of loci showed significant deviations from linkage equilibrium after sequential

Bonferroni correction. However, this did not consistently involve the same pairs and we therefore kept all loci for further analysis.

Table 3.1. Genetic diversity indices per locus for Kalij Pheasant sampled in this population. For each locus, null allele frequency, the average number of alleles (N_A), expected heterozygosity (H_E), observed heterozygosity (H_O), and the inbreeding coefficient (F_{IS}) are provided.

Locus	Null allele freq.	N_A	H_E	H_O	F_{IS}
5C9	0.00%	3	0.519	0.534	-0.011
M1	0.34%	4	0.713	0.682	0.019
2H10	0.47%	3	0.545	0.625	-0.073
3D2	0.00%	2	0.269	0.227	0.081
P17	1.31%	4	0.455	0.455	-0.002
5H2	2.62%	3	0.625	0.625	-0.012
6A5	1.33%	5	0.688	0.663	0.008
2B2	1.04%	2	0.462	0.443	0.018
1G5	2.58%	2	0.306	0.352	-0.072
6D8	0.61%	2	0.498	0.511	-0.017
M2	4.72%	2	0.444	0.386	0.067
4A3	2.43%	3	0.667	0.583	0.063

Relatedness among adults

We calculated maximum likelihood estimates of relatedness among 88 adult Kalij Pheasants in the population, and investigated the genetic relationships among males within a social group. We obtained relatedness results from 17 groups, including the dominant male and 0-4 subdominant males in each group (Table 3.2). Among 32 dyads between within-group dominant and subdominant males, 65.6% were unrelated, 31.2%

were half siblings, and 3.1% were full siblings. Among 24 dyads between within-group subordinate males, 79.2% were unrelated, 16.7% were half siblings, and 4.2% were full siblings.

Table 3.2. Relatedness of within-group male dyads. Dom-Sub relatedness represents the relatedness between the dominant male (Dom-M) and subordinate male (Sub-M) of the group; Sub-Sub relatedness represents the relatedness between one subordinate male and another in the group.

Group	Dom-M	Sub-M	Dom-Sub Relatedness	Sub-Sub Relatedness		
1A10				M181	M200	
	M117	M157	UR	UR	UR	
		M181	UR		HS	
		M200	UR			
2A10				M399		
	M141	M559	HS, FS, PO	UR		
		M399	UR			
BC09	M504	M506	UR			
BC11	MBCd	MBCs	UR			
BN11	M126	M143	UR			
DB10				M167	M191	M192
	M106	M107	HS, FS, PO	UR	UR	UR
		M167	UR		UR	UR
		M191	UR			HS
		M192	UR			
S110				M165	M166	
	M115	M116	UR	UR	UR	
		M165	HS, FS, PO		UR	
		M166	HS, FS			

Table 3.2, continued.

Group	Dom-M	Sub-M	Dom-Sub Relatedness	Sub-Sub Relatedness		
S210				M1SP	M550	M600
	M114	M118	HS, FS	UR	HS	HS
		M1SP	HS, FS, PO		UR	UR
		M550	UR			FS
		M600	UR			
WT10				M304		
	M148	M168	HS, FS, PO	UR		
		M304	HS, FS, PO			
GP11	MGpd	MGps	UR			
H311	M145	M182	HS, FS, PO			
IV11	M170	M538	UR			
SK11				M153		
	M151	M152	UR	UR		
		M153	UR			
Ti11				M2Ti	M3Ti	
	M113	M198	UR	UR	UR	
		M2Ti	UR		UR	
		M3Ti	UR			
TT10	M139	M159	UR			
VT11	M502	M551	HS, FS, PO			
WB11	M1WB	M2WB	FS, PO			

Our rarefaction analyses based on both all individuals and adult-only genotypes suggested little change in mean relatedness estimates when 10 or more loci were involved (Figure S3.1). This indicated that our current sample of microsatellite loci should provide enough power for relatedness estimation.

Offspring parentage

According to CERVUS results, 79 out of 82 offspring sampled from 13 nests were assigned to the putative mother, the female of the group. The three unassigned offspring from three different nests each had two, two and three microsatellite mismatches with the putative mother, which was significantly greater than the average mismatches of 0.07±0.34 (n=82) between offspring and their successfully assigned mother, and was greater than the average number of mismatches of 1.51±1.15 (n = 2465) between randomly paired offspring and females sampled from the population, suggesting these three offspring to be possible brood parasites. Moreover, we cannot find genetic mothers of these three offspring with positive pair LOD scores from other sampled females in the population.

Seventy-eight of 79 offspring mothered by female of the social group were successfully assigned by CERVUS to genetic fathers sampled from the study population (Figure 3.1). While 54 offspring were sired by the dominant male of the social group, 13 offspring were sired by subordinate males from the same social group, 7 were sired by the dominant males from other groups, 4 were sired by a subordinate male from other groups, and for 1 we did not identify a genetic father from sampled males (Table S3.2). Among the 7 offspring sired by a dominant male from other groups, 4 assigned fathers were from groups with home ranges that overlapped the home range of the social group being analyzed, and 3 were from groups whose home range did not overlap with the social group (Zeng et al., unpubl. data). Among the 4 offspring sired by subordinate males from other groups, all 4 assigned fathers were from groups whose home range did not overlap with the focal social group (Zeng et al., unpubl. data).

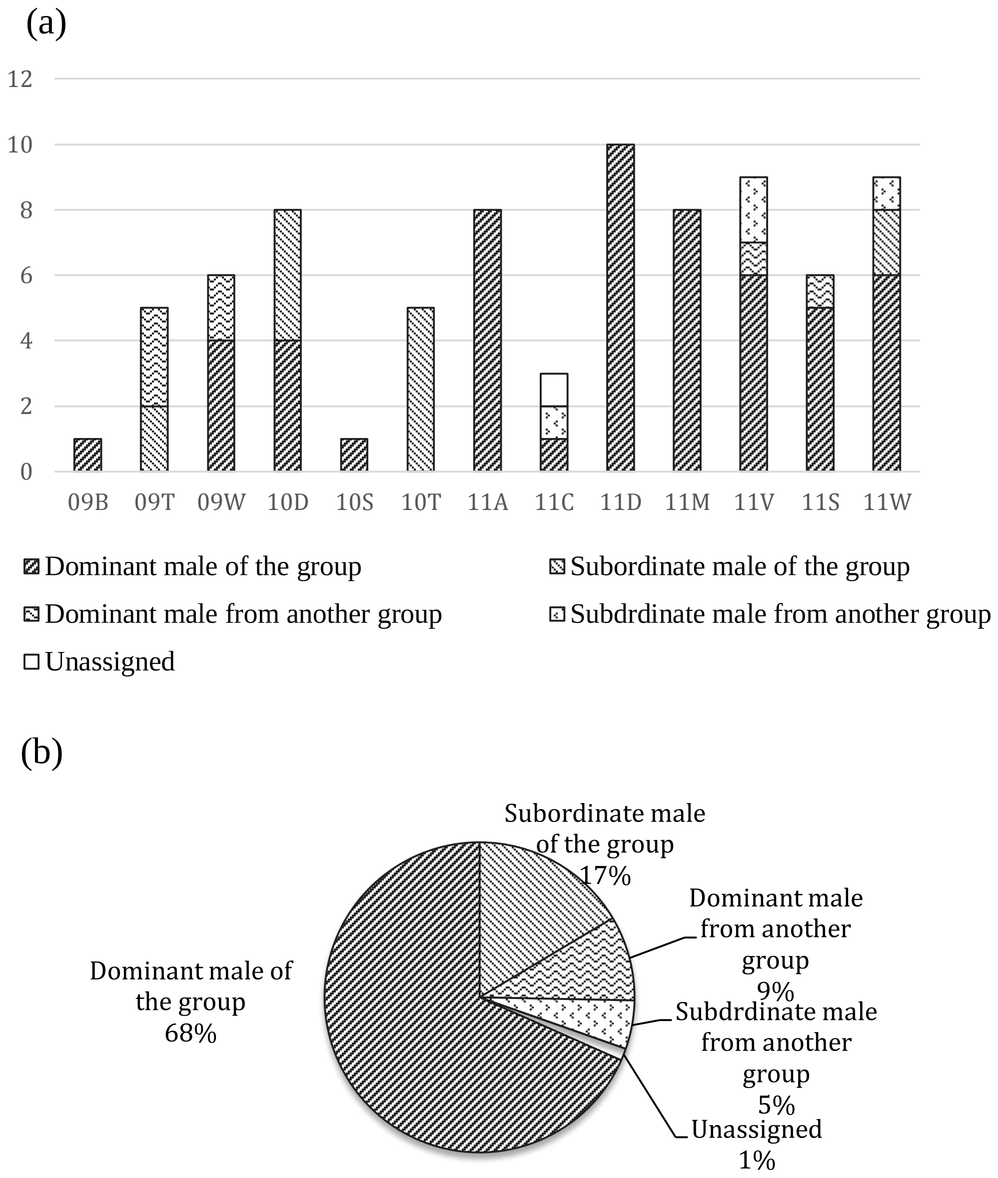

Figure 3.1. (a) Source of assigned genetic fathers of sampled offspring for each brood. The codes on x axis represent sampled brood and Y for numbers of offspring analyzed). (b) Source of assigned genetic fathers of sampled offspring in the population.

Discussion

Our relatedness analyses suggested 34.4% dyads of dominant-subordinate males within groups were related, ranging from unrelated to full siblings. Parentage analysis showed that 68.4% offspring were sired by the dominant male of the group, but some subordinate males from the social group as well as dominant and subordinate males from nearby groups also shared reproduction. Conspecific brood parasitism may have occurred at a very low rate, but our data on this issue were not conclusive.

Kinship patterns in social groups

Although genetic relationship analysis suggested 10 within group dominant-subordinate male dyads to be half siblings, field records suggested 6 of these 10 dyads were more likely parent-offspring, because those subordinate males were hatched when corresponding dominant males were adults. This did not affect our overall results. In this Hawai'ian population of Kalij Pheasant, among 32 with-in group dominant-subordinate male dyads, 34.4% dyads were related, occurring in 8 of the 17 social groups analyzed. Therefore, helpers related to the dominant male can gain inclusive fitness, supporting the hypothesis of kin selection as an important contributing factor in the evolutionary maintenance of cooperative breeding in our study population.

Although relatedness was detected among some group males, the pattern is limited compared to the field observation that most males with family history grew up in the social group, at least after color-banding, which suggest group males may be related to a higher degree. The non-exclusive mating relationship revealed by reproductive share among multiple males, particularly that there were offspring sired by non-group males, can lead to limited relatedness patterns within groups. In addition, two possible ways to form groups with restricted relatedness patterns are through chick-mixing and member recruitments. Chick-mixing occurs when multiple groups with chicks come together and some chicks subsequently follow the wrong group by mistake, which has been documented in precocial birds including species that cooperatively breed such as in Northern Bobwhite *Colinus virginianus* (Faircloth et al. 2005). We suspected chick-mixing in multiple instances when two groups with chicks came into close proximity, and recorded it three times at our study site in 2011, in two groups, confirmed by an increase in chick number (Chapter 1). Such mixing can decrease the level of relatedness among group members. Due to limited field studies, it is not clear what the chick-mixing rate is in their natural range. However, the rate of chick-mixing presumably increases as the group-encounter rate increases at higher population densities. Because the population density at our study site was approximately ten-fold higher than for Kalij and other *Lophura* pheasants in their native ranges (Chapter 1), Kalij Pheasants in

Hawai'i may be more prone to chick-mixing compared to their native counterparts. In addition, recruitment of group members from outside of the group can also decrease the within-group relatedness that we observed. However, we were not able to confirm any recruitment of juveniles due to lack of color-banding on them; we have only observed one incidence of recruitment of one non-group adult male from a nearby group (T. K. Pratt, unpubl. data) at our study site. For all other subordinate males with clear pedigree at the study site, our records show they grew up in the group after banding. Therefore, member recruitments were not likely to have significantly contributed to the limited level of relatedness in the population.

Reproductive share among individuals

Because mating strategies vary greatly among cooperative breeders from helpers who do not mate (e.g., Laughing Kookaburra *Dacelo novaeguineae* (Legge and Cockburn 2000) to every male copulating with the group female (e.g., Galapogos Hawk *Buteo galapagoensis* Faaborg et al. 1995), the influencing factors of reproductive share shall be carefully examined according to specific conditions and constraints of the population. In our study population, although dominant male of the social group fathered the majority (68.4%) of offspring sampled from the population, subordinate males of the social group sired 16.5% of sampled offspring, revealing direct evidence of subordinate males gaining considerable reproductive benefit by staying in a social group, which could not be concluded from field observations. This supports our second hypothesis that helpers gained direct benefit through reproductive share, at least in some cases.

Following Griffith (2002), we considered EPP rate in this cooperative breeding population as paternity outside of the social group. An EPP rate of 14.1% was observed on offspring level, and in 6 out of 13 broods. This rate is higher than the average EPP rate of 5.4% found in non-passerine species (Griffith et al. 2002). High breeding density has been proposed to cause high rates of EPP due to the close proximity to potential mates (Westneat and Sherman 1997). At our study site, population density is exceptionally high compared to the densities reported in the species' native range (Chapter 1), and the degree of home range overlap was also high (Zeng et al., unpubl. data). These findings indicate that females had increased probability of encountering potential mates around their home range and hence increase their opportunity for EPP. Because no data are available on the EPP rate in the native range of Kalij Pheasants, it remains unknown whether such biotic and abiotic ecological factors may influence intraspecific EPP rates.

Interestingly, in 3 of 13 broods in which offspring were all sired by the dominant male of the social group, all putative fathers (which were also the genetic fathers) were not older than 10; in 5 out of 8 broods in which offspring not sired by the putative father was detected, the putative (but not necessarily genetic) fathers were at least 10 years old, while there was no apparent age pattern for the non-putative genetic fathers. While previous research (Chapter 1) demonstrated that males in this population gained dominance through age, the genetic results suggest the possibility that dominant males started to lose reproductive monopoly when they were near the end of their lifespans. Therefore, young subordinate males can stay in a social group to gain future reproductive share, and this may subsequently contribute to the maintenance of cooperative breeding in this population.

Possible conspecific brood parasitism

In birds, the CBP rate is expected to be higher in precocial species compared to altricial species, because precocial species lay larger clutches (Ar and Yomtov 1978), leave nest unattended before full clutch size is reached (Yom-Tov 2001), and parasitic offspring require less care (Sorenson 1992). Although CBP has been reported to occur in more than 200 bird species (Yom-Tov 2001), cases were predominantly from the two precocial groups, Anseriformes and Galliformes. Following the development of non-invasive molecular sampling methodologies (Kreisinger et al. 2010), a handful of in-depth studies have examined CBP in Anseriformes over the last two decades (Åhlund and Andersson 2001; Eadie and Lyon 2011). On the contrary, direct estimates of CBP rate using genetic data are almost absent from Galliformes.

From CERVUS results, we found 3 offspring that were not assigned to the putative mother. For these 3 offspring, we also did not find a sensible genetic father from sampled males in the population. However, it is not sufficient to indisputably conclude conspecific brood parasitism because some mismatches between offspring and their genetic parents can be caused by mutation or genotyping errors (Hoffman and Amos 2005), or some technological pitfalls of using non-invasive egg membrane sampling for genotyping (Kreisinger et al. 2010). Based on the above we suggest that conspecific brood parasitism (CBP) may have occurred in three cases from three separate nests, if we take the more conservative results from CERVUS (genotype mismatch at 2 or more loci), accounting for 3.7% of our sampled offspring. Because we did not find their genetic mother among 28 out of 38 group-affiliated females from which we obtained a blood sample during 2009 to 2011, it is not clear if the three offspring were sired by females from other groups, or non-group-affiliated floater females. Our findings suggest the possibility of CBP in Kalij Pheasant, which may be the second case in the genus *Lophura* (Yom-Tov 2001). Because the CBP data in Galliformes are largely anecdotal, it is difficult to allow direct comparisons of CBP rate over these species. Nevertheless, despite the limited implication of the CBP result, it represents a first step in understanding CBP in Galliformes.

Possible alternative explanations

Among 32 subordinate males in analyzed groups, 11 were related to the dominant male, and 4 subordinate males that were unrelated to the dominant male gained paternity. Kin selection and reproductive share explained cooperation to some extent, but cannot explain it completely. This implies a key role of other potential benefits for helpers. Another alternative explanation that might have contributed to the cooperative breeding of Kalij Pheasants in this population is through natural selection based on the potentially beneficial consequences of group-living (Richardson et al. 2001), such as higher efficiency in finding food and defending the territory (Kokko et al. 2001; Krause and Ruxton 2002), and enhanced survival due to decreased mortality from predation (Alexander 1974; Pen and Weissing 2000). In particular, the semi-isolated forest habitat at our study site represent better resources than large lava fields around the area for the forest-dwelling Kalij Pheasants. Therefore, staying in groups within the forest may be more advantageous than dispersing onto the lava fields or crossing the lava fields in search for suitable forests beyond them.

Conclusions

Overall, our results indicate a mating system with complex reproductive strategies in a precocious bird species introduced to a new environment. As predicted, some subordinate males were related to the dominant male of the social group, but at a lower proportion than field observation implied, possibly due to chick-mixing and group member recruitment. This supported our hypothesis of kin selection as one means by which helpers gained inclusive fitness. Paternity results suggested that the majority of sampled offspring were sired by the dominant male of the social group; however, subordinate males of the group shared some paternity, supporting our hypothesis that helpers gained direct reproductive benefit while staying in the group. Evidence indicated the occurrence of CBP in the population, while our data were not conclusive. The EPP rate was relatively high among non-passerine species, which may be related to high breeding density and large home range overlap in the population. In addition to helpers gaining benefit through kin selection and reproductive share, group-living benefits may have contributed to the evolutionary maintenance of cooperative breeding in this population.

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Supporting Information

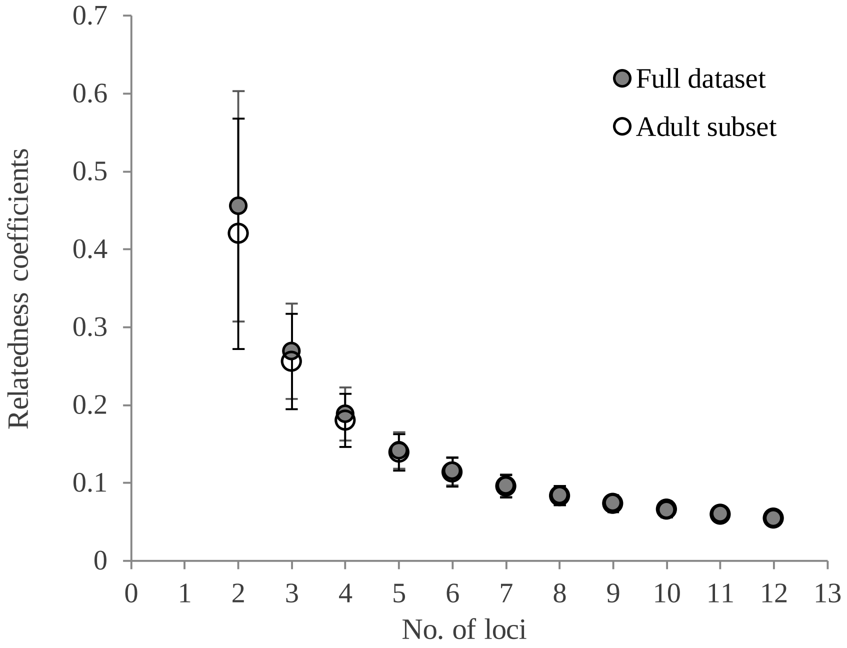

Figure S3.1. Rarefaction analysis suggested little effect on the mean relatedness estimates when 10 or more microsatellites were used, indicating that the marker sets used in this study should provide unbiased estimates.

Table S3.1. Primer multiplex sets for microsatellite amplifications.

Locus name	Allele number	Repeat motif	Size range (bp)	Dye	Reference	Original species	GenBank
5C9	3	$(AC)_{24}$	210-236	ROX	Wang et al. 2009b	*Crossoptilon mantchuricum*	GQ184557
M1	4	$(CA)_{18}$	199-220	FAM	Hennache et al., 2003	*Lophura imperialis*	L43662
4A3	4	$(GA)_{3}AA(GA)_{5}$	188-192	FAM	Wang et al. 2009a	*Syrmaticus reevesii*	FJ221387
2H10	5	$(GT)_{10}$	153-170	ROX	Wang et al. 2009b	*Crossoptilon mantchuricum*	GQ184558
3D2	4	$(CA)_{11}$	281-301	FAM	Wang et al. 2009a	*Syrmaticus reevesii*	FJ221373
5H2	3	$(CA)_{7}$	214-232	FAM	N. Wang, unpubl. data	*Syrmaticus reevesii*	N/A
6A5	5	$(CA)_{11}AC(CA)_{3}$	198–218	ROX	Wang et al. 2009a	*Syrmaticus reevesii*	FJ221381
2B2	3	$(GA)_{10}$	160-165	HEX	N. Wang, unpubl. data	*Syrmaticus reevesii*	N/A
1G5	2	$(CA)_{15}$	181-194	FAM	Wang et al. 2009a	*Syrmaticus reevesii*	FJ221378
6D8	2	$(CA)_{13}$	121-132	FAM	N. Wang, unpubl. data	*Syrmaticus reevesii*	N/A
M2	3	$(CA)_{10}$	294-300	HEX	Hennache et al., 2003	*Lophura imperialis*	G32005
P17	4	$(TG)_{7}$	169-192	FAM	Dong et al., 2013	*Lophura nycthemera*	N/A

Table S3.2. Group composition and parentage result for 82 offspring from 13 groups. Putative mom is the female of the social group; putative dad is the dominant male of the social group. Genetic mom is the genetic mother identified by CERVUS; genetic dad is the genetic father assigned by CERVUS. GD represents dominant male from the social group; GS represents a subordinate male from the social group; NGD represents a dominant male from other than the social group; and NGS represents a subordinate male from other than the social group.

Group Name	Putative Mom	Putative Dad	Group Subordinate Males	Offspring	Genetic Mom	Genetic Dad	Source
BC09	F246	M506	M504	09B2	F246	M506	GD
TT09	F009	M139	M159	09T2	F009	M144	NGD
				09T5	F009	M144	NGD
				09T6	F009	M159	GS
				09T7	F009	M144	NGD
				09T8	F009	M159	GS
WT09	F211	M148	M168	09W1	F211	M148	GD
				09W2	F211	M138	NGD
				09W3	F211	M148	GD
				09W4	Not found	Not analyzed	
				09W5	F211	M148	GD
				09W6	F211	M148	GD
				09W7	F211	M138	NGD
DB10	F053	M106	M107, M167, M191, M192	10D1	F053	M107	GS
				10D2	F053	M106	GS
				10D3	F053	M107	GD
				10D4	Not found	Not analyzed	
				10D6	F053	M107	
				10D7	F053	M106	GS
				10D8	F053	M106	GD
				10D9	F053	M106	GD
				10D0	F053	M107	GD
TT10	F301	M139	M159	10T1	F301	M159	GS
				10T2	F301	M159	GS
				10T3	F301	M159	GS
				10T4	F301	M159	GS
				10T5	F301	M159	GS

Table S3.2, continued.

Group Name	Putative Mom	Putative Dad	Group Subordinate Males	Offspring	Genetic Mom	Genetic Dad	Source
S110	F206	M116	M115, M165, M166	10S6	F206	M116	GD
1A11	F084	M157	M181	11A1	F084	M157	GD
				11A2	F084	M157	GD
				11A3	F084	M157	GD
				11A4	F084	M157	GD
				11A5	F084	M157	GD
				11A6	F084	M157	GD
				11A7	F084	M157	GD
				11A8	F084	M157	GD
CS11	FCrs	M559	NA	Crs1	FCrs	Not found	
				Crs2	FCrs	M143	NGS
				Crs3	FCrs	M559	GD
DB11	F053	M107	M192, M191, M167	11D1	F053	M107	GD
				11D2	F053	M107	GD
				11D3	F053	M107	GD
				11D4	F053	M107	GD
				11D5	F053	M107	GD
				11D6	F053	M107	GD
				11D7	F053	M107	GD
				11D8	F053	M107	GD
				11D9	F053	M107	GD
				11D0	F053	M107	GD
H311	F099	M145	M182	11H1	F099	M145	GD
				11H2	Not found	Not analyzed	
				11H3	F099	M145	GD
				11H4	F099	M145	GD
				11H5	F099	M145	GD
				11H7	F099	M145	GD
				11H8	F099	M145	GD
				11H9	F099	M145	GD
				11H0	F099	M145	GD

Table S3.2, continued.

Group Name	Putative Mom	Putative Dad	Group Subordinate Males	Offspring	Genetic Mom	Genetic Dad	Source
IV11	F100	M538	M170	Ivy1	F100	M1SP	NGD
				Ivy2	F100	M538	GD
				Ivy3	F100	M538	GD
				Ivy4	F100	M118	NGS
				Ivy5	F100	M538	GD
				Ivy7	F100	M538	GD
				Ivy10	F100	M538	GD
				Iv11	F100	M538	GD
				Iv12	F100	M118	NGS
S311	F062	M399	M-UB	11S1	F062	M399	GD
				11S2	F062	M399	GD
				11S3	F062	M399	GD
				11S4	F062	M399	GD
				11S5	F062	M157	NGD
				11S6	F062	M399	GD
WT11	F049	M148	M168, M304	11W1	F049	M148	GD
				11W2	F049	M168	GS
				11W3	F049	M148	GD
				11W4	F049	M304	GS
				11W5	F049	M148	GD
				11W6	F049	M148	GD
				11W7	F049	M148	GD
				11W8	F049	M148	GD
				11W9	F049	M170	NGS

General Discussion

I studied the social behaviors, genetic social structure, and reproductive strategies of Kalij Pheasants at Kipuka Puaulu in Hawai'i Volcanoes National Park from 2009 to 2011. Kalij Pheasants in the study population formed social groups containing one female and one to six males. More multiple-male groups existed than pairs. Larger groups occupied larger home ranges in general. All adults in social groups performed cooperative behaviors including caring for chicks, defending against conspecific intruders, and exhibiting vigilance against predators. While the adult sex ratio was biased toward males with an average of M:F = 2.10, primary and secondary sex ratios revealed from egg samples were not biased. An average density of 3.21 residents/ha appeared 10-fold higher than in closely related species in their native range, indicating that breeding habitat in the kipuka is likely saturated. Removal of 12 of 29 groups resulted in some subordinate males leaving their former group and establishing a new group with mostly previously unaffiliated (floater) females, and hence to a decrease in the average group size in in the population. Genetic examination revealed 34.4% of subordinate males were related to the dominant male of the group. While dominant males in social groups fathered 68.4% of offspring sampled from the population, 16.5% of offspring were sired by subordinate males of the social group, and 14.1% offspring were sired by males not from their social group. Following Griffith (2002), we consider the latter two values the extra-pair paternity rate in this population. Likely conspecific brood parasitism was identified at a rate of 3.7%, but our data were not conclusive on this matter.

I attempted to address the two fundamental questions in understanding the evolution of cooperative breeding: "why do helipers stay" and "why do they help" (Stacey and Koenig 1990). For the first question, we tested the possible influence of habitat saturation and mate limitation on cooperative breeding of Kalij Pheasants in the study population through the removal experiment. Due to the significant decline in the number and proportion of multiple-male groups post-removal, and to the fact that the number of groups before and after removal was equivalent, I conclude that habitat saturation was, indeed, essential. Most subordinate males who left their original groups acquired previously unidentified female mates lacking any observed previous group affiliation (i.e., floaters) and formed new breeding groups. Therefore, I conclude that mate limitation was not a critical limiting factor preventing subordinate males from leaving the social group. However, four groups consisted a single male with no female mates after removal, indicating that the availability of female mates prevented some males from independently breeding after available females were depleted. A common challenge to determining the significance of ecological constraints in limiting independent breeding in cooperatively breeding species or populations is that ecological constraints are ubiquitous in nature (Heinsohn et al. 1990), but cooperative breeding is not. In fact, the cause for cooperative breeding can be complex and cooperative breeding is more likely the result of a combination of factors. It is helpful to examine a cooperative breeding system also from other perspectives, such as what benefits did helpers gain, i. e., “Why do they help.”

My genetic analyses showed 11 of 32 subordinate males (34.4%) from 8 of the 17 social groups analyzed were related to the dominant male of the group. Although this rate was lower than expectation derived from field observation, it indicated that these helpers can gain inclusive fitness, and that kin selection may play a role in maintaining cooperative breeding in this study population. At the same time, subordinate males of the social group sired 16.5% of sampled offspring. Such evidence of reproductive share suggested that direct benefit gained by helpers might also contribute to the evolutionary maintenance of cooperative breeding in this population. Although dominant males possessed the majority of offspring parentage in this population and the reproductive share by subordinate males was comparatively low, subordinate males will likely gain dominance through age, and subsequently increase their reproductive share in the group.

Reports of cooperative breeding in Galliformes are rare. The more prevalent form of cooperative breeding in Galliformes seems to be communal breeding found in some quails (e.g., Gambel’s Quail *Callipepla gambelii*, Brown et al. 1998; California Quail *Callipepla californica*, Lott and Mastrup 1999; Northern Bobwhite *Colinus virginianus*, Brooks and Rollins 2007) and an intermediate form between communal breeding and helpers-at-the-nest observed in a few Eared-Pheasants (Lu and Zheng 2005).

Helpers-at-the-nest (Brown 1987) occurred in my study population of Kalij Pheasants, as well as a Buff-throated Partridge *Tetraophasis szechenyii* population studied by Xu et al. (2010) and Black-breasted Wood-Quail *Odontophorus leucolaemus* studied by Hale (2006). In all three species, stable social groups occupied year-round home ranges and group members participated in active defense of them, while in some other cooperative Galliformes, groups appeared migratory to some extent. It is not clear how or if this sedentary lifestyle influenced their social behaviors. As evidence accumulates, cooperative breeding in precocial species can provide a different perspective that helps to illustrate the factors involved in the evolutionary maintenance of cooperative breeding in the absence of the demands of intensive offspring care required in altricial species. Currently, studies of the lifetime fitness consequences of breeders and helpers in precocial species are limited. Such examinations are much needed and can shed light into the causes and consequences of cooperative breeding in general.

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