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Animal behaviour

Emergent social structure is typically not associated with survival in a facultatively social mammal

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For social animals, group social structure has important consequences for disease and information spread. While prior studies showed individual connectedness within a group has fitness consequences, less is known about the fitness consequences of group social structure for the individuals who comprise the group. Using a long-term dataset on a wild population of facultatively social yellow-bellied marmots (*Marmota flaviventer*), we showed social structure had largely no relationship with survival, suggesting consequences of individual social phenotypes may not scale to the group social phenotype. An observed relationship for winter survival suggests a potentially contrasting direction of selection between the group and previous research on the individual level; less social individuals, but individuals in more social groups experience greater winter survival. This work provides valuable insights into evolutionary implications across social phenotypic scales.

1. Introduction

An individual's social phenotype has important implications for its fitness in group-living species [1]. Survival, an important fitness correlate, is influenced by the degree, rate and context of social interactions in some species, as measured by social network analysis. For example, stronger social relationships have been associated with greater survival in male bottlenose dolphins (*Tursiops* sp.; [2]), chacma baboons (*Papio hamadryas ursinus*; [3]), Barbary macaques (*Macaca sylvanus*; [4,5]) and feral horses (*Equus caballus*; [6,7]). Several mechanisms contribute to this positive sociality–survival relationship, such as predator defence and detection [8–10] and resource exploitation [11,12]. Yet, higher rates of sociality can also be costly in terms of survival, as seen in female bottlenose dolphins [2] and is often associated with predator attraction and disease acquisition [13–15].

This previous work exclusively explored the fitness consequences of an individual's social phenotype, leaving the consequences of the group social phenotype unstudied [16–18]. Group social structure—emergent network traits generated by the interactions of all group members—quantifies the group social phenotype in a way more complex than averages of individual-level network values [19–22]. Social structure influences key ecological and evolutionary processes [23] such as group formation and regulation [24] and movement patterns [25]. Social structure is in turn influenced by ecological conditions [26,27] and group composition of individual social and non-social phenotypes [28,29]. In most species, social structures are non-random, repeatable across years, group compositions, and environmental gradients and conditions [18,29–37].

Social structure may also have fitness consequences. Captive bluebanded gobies (*Lythrypnus dalli*), an obligately social species, have reduced reproductive success when living in groups with more reciprocated aggressive interactions

Table 1. Measures of social structure with the *a priori* hypothesized direction of the relationship.

measure	description	references	interpretation	summer hypothesis	winter hypothesis
density	number of interactions observed represented as a fraction of all possible interactions	Burt [46]; Wasserman & Faust [20]; Grund [47]	how connected a group is	+	−
transitivity	proportion of completely connected triads out of the total possible triads	Wasserman & Faust [20]; Milo *et al*. [48]; Faust [49]	how cyclically connected a group is. There are more transitive components in affiliative networks in this system [50]	+	−
reciprocity	the number of mutual interactions divided by the number of possible mutual interactions	Wasserman & Faust [20]; Kankanhalli *et al*. [51]; Squartini *et al*. [52]	used to quantify how mutual or one-sided interactions are in a group	+	+
degree assortativity	tendency for social ties to share similar individual degree measures	McPherson *et al*. [53]; Currarini *et al*. [54]	how socially homogeneous a group is, in terms of individual's number of social partners	+	+
average path length	average of the shortest paths between all pairs of nodes	Watts & Strogatz [55]; Broder *et al*. [56]	identifies the size of a network, in addition to raw group size	−	+
cut points	number of social ties that if cut will result in two or more separate networks	Wasserman & Faust [20]; Borgatti [57]	how stable or fragmentable (breakable) a group is	−	+

[38]. In wild yellow-bellied marmots, adult female reproductive success modestly increases when living in more fragmentable social groups [39]. Adults also gain body mass more slowly when living in more connected groups, though yearlings gain mass more quickly in socially homogeneous groups [40]. These studies highlight how social structure may have different fitness consequences across species, demographic roles and social systems [16,17]. However, how social structure specifically relates to patterns of survival in animal populations is not understood.

We explored the relationship between group social structure and survival over both the active summer season and winter hibernation in a long-studied population of yellow-bellied marmots. In this system, an individual's social phenotype predicts survival [41,42] and other fitness correlates (alarm call propensity: [43]; reproductive success: [44]; longevity: [45]). Informed by previous work on the individual and group levels in this system, we developed *a priori* hypotheses (table 1) for six network measures, capturing the connectedness, mutuality and homophily of a group, and both summer and winter survival. Females living in larger social groups and yearling females engaging in more social interactions experience enhanced summer survival [42]. Predation is the primary driver of summer mortality in this system [58], thus more social individuals, or those residing in more connected groups, may better detect and avoid predators [8–10]. We predict that residing in more connected, reciprocal and socially homogeneous groups will be associated with increased summer survival. However, more social marmots are less likely to survive hibernation [41]. Since body condition is the primary driver of winter mortality, this may be a function of social interaction time costs [59] and/or individuals in groups having more costly periodic arousals during social hibernation [60,61]. Thus, we predict that residing in more connected, less reciprocal and socially heterogeneous groups will be associated with decreased winter survival, as was seen for mass gain and reproductive success [39,40].

2. Methods

(a) Study system

Yellow-bellied marmots are harem-polygynous, facultatively social ground-dwelling squirrels living in matrilineal colonies with one to two territorial males [62,63]. The population at the Rocky Mountain Biological Laboratory in Colorado (38°57′N, 106°59′W; *ca* 2900 m elevation) has been continuously studied since 1962. These marmots are active for five months annually (mid-April to mid-September). Following their winter hibernation, they mate soon after emergence with yearlings dispersing and new pups emerging in late-June to early-July. Annually, most males and about half of females disperse as yearlings, typically resulting in movement out of the study area [63]. We only explore adult summer and winter survival because yearling dispersal creates uncertainty about yearling survival.

(b) Data collection

We repeatedly trapped and observed marmots during their active season from 2002 to 2020. All individuals studied in our population have unique non-toxic dye marks on their dorsal pelage, allowing accurate identification of interacting individuals and precise estimates of survival. A detailed ethogram and behavioural observational methodology are outlined in Blumstein *et al*. [64]. The initiator, recipient, location, time and type of each interaction is recorded, with most interactions (79%) occurring between identified individuals. The remaining 21% interactions could not be identified because of interacting individuals' posture or visual obstructions. We excluded these interactions from our data, which should not significantly influence our estimates of social structure [65].

Only adults and yearlings are included in our social interaction data because only these cohorts were present in spring, when social interactions were most common. Pups were excluded because of their mid-season emergence and primary interaction with their mother and each other [66]. We eliminated transients by excluding individuals observed or trapped fewer than five times in a given year [41,43–45]. Colony sites are grouped into higher and lower elevation sites (five are at higher and seven are at lower elevation sites). Higher elevation sites are approximately 166 m higher and experience harsher weather conditions [36,67,68].

(c) Social network measures

Directed and weighted interaction matrices were constructed from affiliative interactions for each year (2002 to 2020) the package 'igraph' (version 1.3.5; [69]) for R 4.2.0 [70]. We focused on affiliative interactions (e.g. allogrooming, greeting and play) because they relate to summer and winter survival on the individual level [41,42] and affiliative interactions comprised 88% of interactions. These affiliative matrices consisted of 38 968 social interactions between 726 individuals (626 of whom were observed across multiple years). A social group is defined as a network component (set of connected individuals with no other external connections) appearing naturally within a valley location (higher elevation or lower elevation) in a given year. This operationalization produced 137 social groups with group sizes ranging from 3 to 58 individuals with a mean of 20.51 (s.e. = 0.52). Details on identical behavioural observation and network methods can be found in Philson & Blumstein [39].

Six social network measures were calculated for each group to quantify social structure (table 1). Density, transitivity, average path length and cut points quantify connectivity; reciprocity and degree assortativity quantify homophily. We selected these measures due to their importance in our system [39,40,50], other systems [18,27,38,71], and because these network measures have analogous measures on the individual level (e.g. density and degree; transitivity and clustering coefficient; [18]), aiding our understanding of consequences of social behaviour across social phenotypic scales [20]. The reliability of the social network measures is facilitated by our observations of marmot social groups across their entire active season (mean n observations per individual across years = 28.81, range of each year = 6.79– 75.14) and low rate of unknown individuals involved in social interactions [65,72,73]. Because group size is associated with many marmot social network measures (e.g. density, cut points; [35,39,40]), we standardized each measure not already 'standardized' (i.e. degree assortativity and cut points) by dividing the network measures by group size [20,39,40].

(d) Data analysis

Summer survival was defined as individuals seen or trapped after 1 August or in the following years. Winter survival was defined as individuals seen the following year/s. Survival data were paired with network measures from the current active season (for summer survival) or the active season before hibernation (for winter survival). We fitted two generalized linear mixed models (summer and winter) with a binomial distribution and a bobyqa optimizer with 20 000 iterations using 'lme4' [74,–76]. Model assumptions and zero inflation were checked after fitting. The summer survival model included the six network measures, social group size, age, sex, June mass, valley location and a predation index as fixed effects. The winter survival model included the six network measures, group size, age, sex, August mass, valley location, and the date bare ground was first visible because of melting snowpack in the centre of our colony areas. Models had 559 observations consisting of 252 unique individuals in 91 social groups across 19 years.

We included the individual attributes age, sex, mass and location because survival is multi-causal and we wished to account for important attributes with known fitness implications [77–79]. Group size was included due to its relationship with fitness correlates in this system [35,44]. Predation index is a binary variable calculated by whether the number of predators observations at that colony was below or above the median number of predator observations across all colony areas in that year [80], providing a value relative to all other years [42]. Individual ID and year were included as random effects to account for annual environmental and demographic differences [36,81,82] and individuals observed over multiple years.

All continuous variables were standardized (mean-centred and divided by 1 s.d. using the 'scale' function in base R; [83]). Group size was log10 transformed before scaling, but we employed no other transformations. We checked for multi-collinearity between fixed effects and found each had a correlation coefficient of less than 0.8 [84,85], though both density and group size had a VIF of greater than 5 in both the summer and winter models (electronic supplementary material, table S1). Because group size has known relationships with fitness in this system [35,39,40,44], we removed density from both models and the interpretation of the results for the measures of social structure did not change (electronic supplementary material, table S2). Since this suggests our models were relatively robust, we report models that included both density and group size here.

Marginal and conditional R^2 values for each model and the semi-partial marginal and conditional R^2 that estimate variance explained by each fixed effect were calculated using 'partR2' [86,87]. We estimated 95% confidence intervals for our R^2 values using 100 parametric bootstrap iterations. Figures were generated with 'ggplot2' [88].

3. Results

Contrary to our *a priori* hypothesis, we found a statistically significant negative main effect of cut points on winter survival ($B = -0.359$; $p = 0.031$; s.e. = 0.167; figure 1; table 2), suggesting individuals residing in more fragmentable—breakable into two or more separate groups of two or more individuals—social groups experienced reduced winter survival. Overall, five of the six measures of social structure did not have a significant statistical relationship with winter survival, suggesting the relationship is modest. This model had a marginal R^2 value of 6.28% and a conditional R^2 value of 7.93%. Cut points explained 1.11% of the marginal semi-partial R^2 variance further suggesting the relationship is modest.

Rejecting our *a priori* hypotheses, we found no significant main effects of social structure in our summer survival model (figure 2; table 2), suggesting social structure does not play a primary role in summer survival. This model

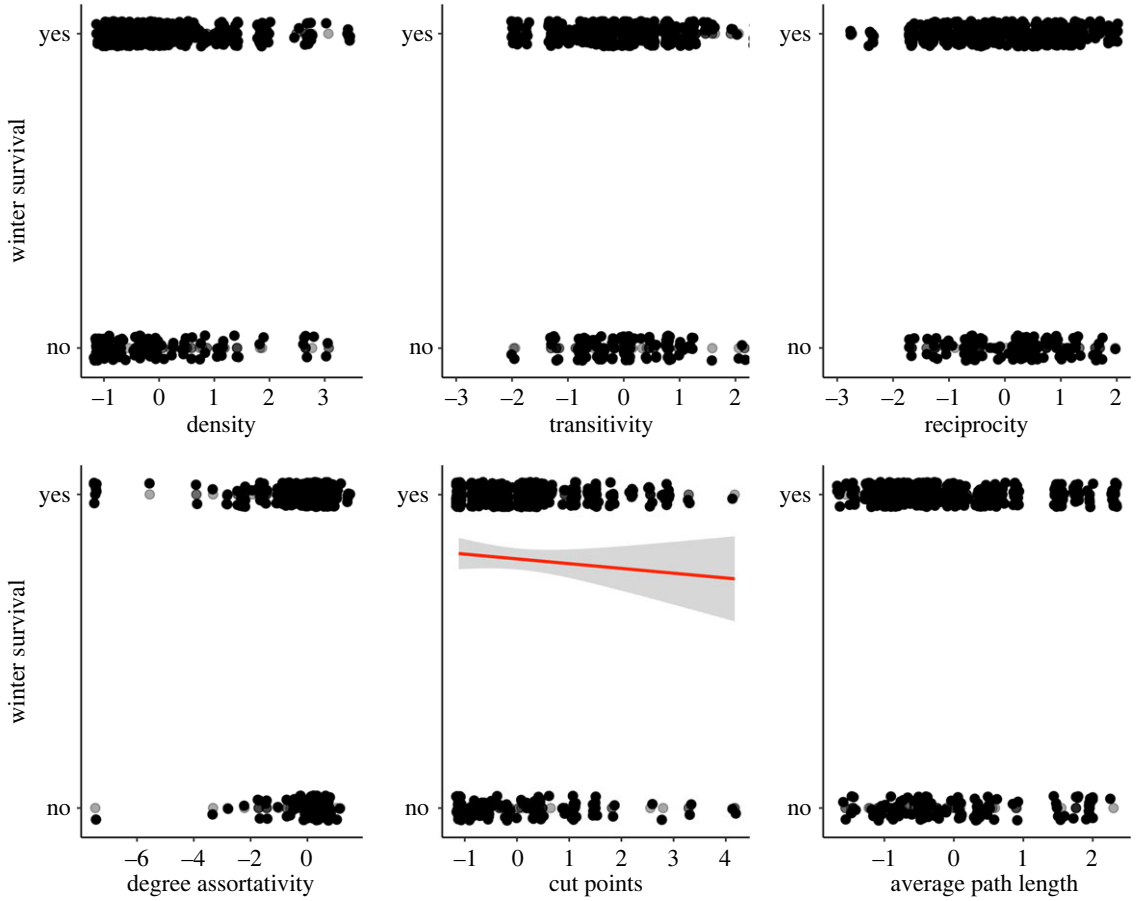

Figure 1. Relationship between winter survival and social structure. The predictor variable is scaled. Darker points indicate overlaid data.

explained 7.39% of the marginal variance and 19.17% of the conditional variance.

4. Discussion

We found no strong and consistent evidence that social structure is related to summer survival in this system. However, because one measure of social structure (cut points) was related to winter survival, group structure may have a limited impact in specific contexts. Because group social structure exists on a larger, emergent phenotypic scale than an individual's direct social interactions [16,22,89], it is logical that the relationship between social structure and fitness may be quite modest because of its indirect nature, as seen in previous work [18,38,39].

Social structure not relating to summer survival is surprising given that more connected groups might excel at predator detection and/or avoidance [8–10,90,91]. However, the lack of a statistically significant relationship may result from the emergent, and hence indirect nature of social structure [18–22]. Since these facultatively social marmots experience mostly fitness costs from more social individual and group phenotypes [39–41,43–45], the consequences of more social individual phenotypes may not scale linearly to the group social phenotype, as seen in male forked fungus beetles [18]. That is, residing in a more connected group may not incur the same benefits as increased individual sociality. A marmot may have modest benefits at an individual level of being more socially connected with others, but still regulate their social interactions by residing in less connected groups. Because of the few associations with winter survival, the strength of group-level selection is likely less than the strength of individual-level selection for survival in this system. However, targeted exploration of multi-level selection is required to specifically test this hypothesis.

Interestingly, the one statistically significant relationship we identified (between winter survival and cut points) may have interesting evolutionary implications and further suggests that the individual social phenotype may not scale to the group phenotype [18]. In this system, more socially connected individuals have decreased winter survival [41], suggesting selection acts against more social individual phenotypes. As we have shown here, individuals residing in less fragmentable (or more closely socially connected) groups have increased winter survival, suggesting selection acts towards more social group phenotypes. The mechanisms for this are entangled. Winter survival is closely associated with body mass [81]. Thus, more social individuals in more social groups may have less time to forage to develop energy reserves and may be more likely to socially hibernate, increasing the risk of costly torpor interruptions [60,61]. However, residing in a less fragmentable group, where individuals may be more likely to share space and hear conspecific alarm calls [26,27,30,92] may facilitate predator avoidance and allow for more time to gain mass. This potential explanation is muddled, but not dismissed, by the lack of an observed relationship for summer survival.

Importantly, residing in a less fragmentable group does not necessarily imply that individuals within that group are significantly more social [19–22]. This also does not imply more connected social structures are beneficial in this species

Table 2. Model estimates, standard error, *p*-value, marginal and conditional and semi-partial part R^2. Italic *p*-values indicate $p < 0.05$.

	winter survival					summer survival			
	Est. ± s.e.	*p*-value	*marginal* partR^2 (%)	conditional partR^2 (%)		Est. ± s.e.	*p*-value	*marginal* partR^2 (%)	conditional partR^2 (%)
intercept	0.968 ± 0.188	*<0.001*	6.28 (5.47–14.53)	7.93 (5.66–19.59)	intercept	1.91 ± 0.449	*<0.001*	7.39 (3.04–18.84)	19.17 (7.46–94.49)
density	−0.229 ± 0.346	0.508	0.02 (0–8.66)	1.66 (0–14.04)	density	0.848 ± 0.601	0.158	0.88 (0–12.56)	12.66 (1.06–94.03)
transitivity	−0.163 ± 0.233	0.485	0.17 (0–8.81)	1.82 (0–14.18)	transitivity	0.021 ± 0.312	0.947	0.02 (0–11.72)	11.8 (0.4–93.97)
reciprocity	−0.119 ± 0.172	0.49	0.36 (0–8.98)	2.01 (0–14.34)	reciprocity	−0.26 ± 0.225	0.247	0.95 (0–12.62)	12.72 (1.12–94.04)
degree assortativity	0.093 ± 0.16	0.563	0.09 (0–8.73)	1.74 (0–14.11)	degree assortativity	0.173 ± 0.244	0.477	0 (0–11.69)	11.76 (0.38–93.97)
cut points	−0.359 ± 0.166	*0.031*	1.11 (0.23–9.68)	2.75 (0.33–15)	cut points	−0.069 ± 0.21	0.742	0 (0–11.6)	11.67 (0.34–93.96)
average path length	0.125 ± 0.239	0.602	0 (0–8.65)	1.65 (0–14.03)	average path length	0.589 ± 0.322	0.067	0.73 (0–12.41)	12.51 (0.91–94.02)
group size	−0.665 ± 0.286	*0.02*	1.25 (0.37–9.81)	2.9 (0.48–15.13)	group size	−0.466 ± 0.421	0.269	0 (0–11.47)	11.54 (0.29–93.95)
valley location	0.087 ± 0.131	0.508	0.19 (0–8.82)	1.84 (0–14.19)	valley location	0.283 ± 0.219	0.196	0.88 (0–12.55)	12.66 (1.05–94.03)
sex	0.709 ± 0.18	*<0.001*	3.24 (2.39–11.68)	4.88 (2.56–16.89)	sex	0.699 ± 0.223	*0.002*	1.89 (0.28–13.53)	13.67 (2.04–94.1)
age	−0.076 ± 0.122	0.531	0.1 (0–8.74)	1.75 (0–14.11)	age	−0.137 ± 0.227	0.546	0.44 (0–12.13)	12.22 (0.62–94)
August mass	0.525 ± 0.172	*0.002*	1.94 (1.07–10.46)	3.59 (1.2–15.74)	June mass	0.62 ± 0.31	*0.045*	0 (0–11.45)	11.51 (0.28–93.95)
date of snowmelt	−0.122 ± 0.142	0.39	0.23 (0–8.86)	1.88 (0–14.23)	predator index	0.066 ± 0.184	0.718	0 (0–11.64)	11.71 (0.36–93.96)

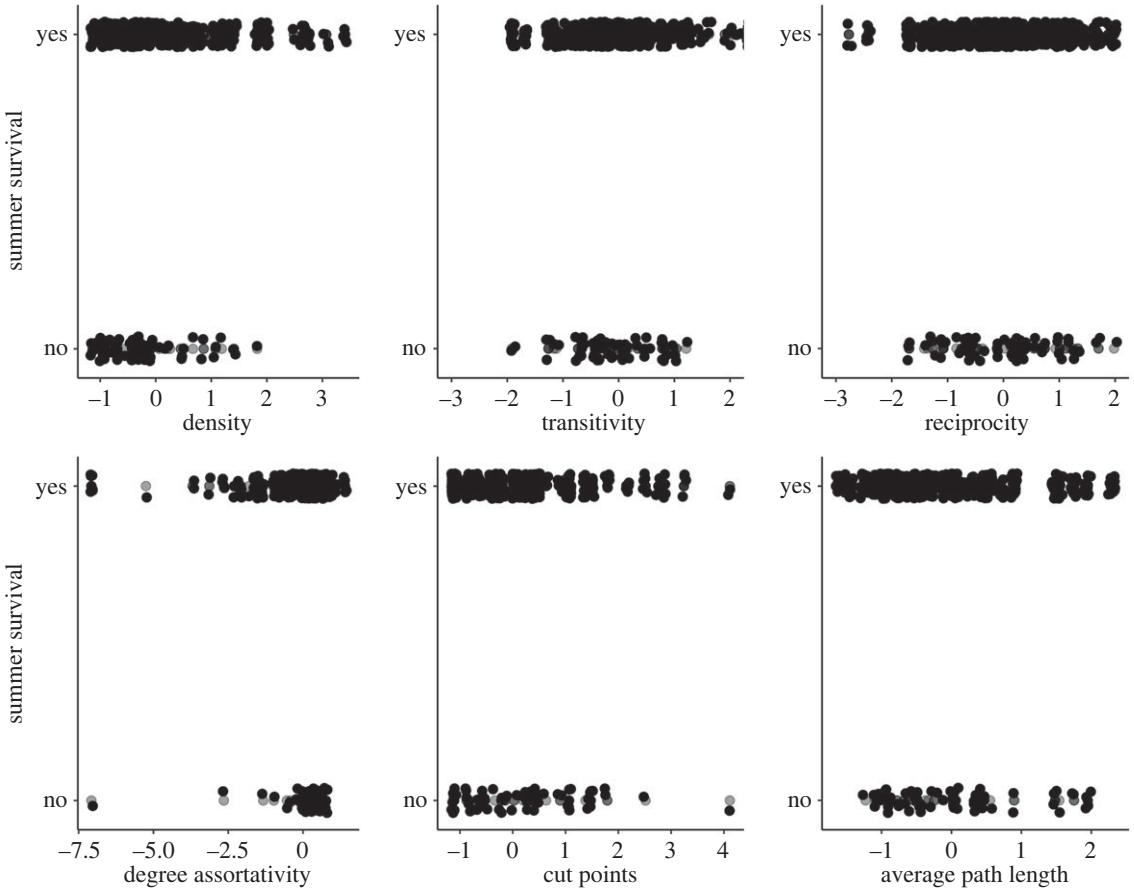

Figure 2. Relationship between summer survival and social structure. The predictor variable is scaled. Darker points indicate overlaid data.

[39,40], but rather that in specific contexts some benefits to increased sociality may emerge at different social scales. As mentioned, the strength and potential contrasting direction of selection between individual and group traits in this system requires further exploration. Opposing selection has been observed across species for non-social traits [71,93–98], though less research investigates selection acting on social behaviour across social scales [95,96,99]. Bluebanded gobies [38], chacma baboons (*Papio hamadryas ursinus*; [3]) and social bumblebees (*Bombus* sp.; [100,101]) experience fitness benefits across social scales. However, not all species may experience, or experience via the same mechanisms, aligned fitness consequences across social scales [18].

Understanding the evolution of social behaviour requires directly measuring the fitness consequences of natural behavioural variation [38]. While the ranging fitness consequences of individual social network position is well documented [2,16,102–106], growing research supports group-level social network traits also have a range of fitness consequences across species [18,38–40]. This work highlights evolutionary implications across social scales and our main finding is that group social phenotype has a complex relationship with fitness that does not necessarily scale. Our observed relationship may further suggest complexity via contrasting selection between the individual and group social phenotypes on winter survival. However, because the relationship is modest and little research investigates selection acting on behaviour across social scales, future work using a multi-level selection approach is essential to better understand the adaptive value of sociality.

Data accessibility. Data and code to replicate analyses are available from OSF at https://doi.org/10.17605/OSF.IO/T93E8 [107].

Data are provided in the electronic supplementary material [108]

Authors' contributions. C.S.P.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, visualization, writing—original draft and writing—review and editing; D.T.B.: conceptualization, formal analysis, funding acquisition, investigation, methodology, project administration, resources, supervision, writing—original draft and writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no conflicts of interest.

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