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## ENDOCRINE ASPECTS OF FEMALE-FEMALE PAIRING IN THE WESTERN GULL (*LARUS OCCIDENTALIS WYMANI*)

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**Abstract.** Investigations of the colonies of western gulls on Santa Barbara Island, California, have revealed a surplus of females and the occurrence of female-female pairs that produce clutches with as many as six eggs. Females are able to establish and defend breeding territories, behaviours generally thought to be under the control of androgens. There are very few significant differences in circulating levels of the luteinizing hormone and androgens among breeding males, breeding females in heterosexual pairs, and breeding females in homosexual pairs. In contrast, however, only females sampled in 1977, in both homo- and heterosexual pairs, have elevated plasma levels of oestrogens, in spring, coincident with the period in which they show courtship behaviours such as food begging and solicitation of copulation. Given a sex ratio skewed in favour of females, as is apparently the case with the colonies of this species on Santa Barbara Island, and the essentially equal plasma levels of androgens in males and females, it is not difficult to rationalize the formation of female-female pairs. Our findings do not support the hypothesis that female-female pairing involves hormonal masculinization of one member of the pair.

The demonstration by Hunt & Hunt (1977) of a significant fraction of female-female pairs in the breeding population of western gulls (*Larus occidentalis wymani*) on Santa Barbara Island, has motivated questions concerning the origin and nature of this phenomenon, which led us to formulate two mutually non-exclusive hypotheses. The first assumed that female-female pairing occurs, at least in part, because of a surplus of females. Investigation of the sex ratio of birds of breeding age in the colony on Santa Barbara Island has lent support to this hypothesis (Hunt et al. 1980). The second hypothesis proposed that homosexual female pairs form because of endocrine and behavioural masculinization of one member which then assumes the male role in the pair. However, observations of overall territorial and mating behaviour (G. L. Hunt, Jr., A. L. Newman, M. H. Warner, J. C. Wingfield & J. Kaiwi, unpublished data) do not support this hypothesis, although in a restricted set of courtship behaviours there are differences in the roles played by members of homosexual pairs. In the Laridae, as in many other groups of birds, it is generally thought that the role of the male involves establishment of breeding territory, attraction of a female mate and courtship, and furthermore, that these be-

haviours are at least partially dependent on circulating androgens (Boss 1943; Cheng & Lehrman 1975; Terkel et al. 1976; cf. also Farner & Wingfield 1980; Wingfield & Farner 1980). Nevertheless, female-female pairs of western gulls establish and maintain breeding territories, often for a period of several years, and engage in most of the usual courtship behaviours, e.g. occasionally one female will mount the other and attempt to copulate (G. L. Hunt, Jr., A. L. Newman, M. H. Warner, J. C. Wingfield & J. Kaiwi, unpublished data). It is for this reason that it seemed possible that one of the females of the homosexual pair had undergone endocrine masculinization. As an examination of this possibility we present herein the results of an investigation of the circulating levels of gonadal hormones in breeding males, and homosexually and heterosexually paired breeding females. Some of the results communicated herein have been included in condensed form in a brief preliminary communication (Wingfield et al. 1980b).

### Methods

The major focus of the study was on the colony on the northwest slope of Santa Barbara Island. In 1977 and 1978 over 400 western gulls were captured with a cannon net to which they were lured by cooked popcorn. When at least 10 were lured by the food, the cannons were fired electrically, extending the net over the birds. We captured as many as 75 gulls per shot.

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During the nesting phase, gulls were also captured by placing a noose of 18-kg test fishing line around the nest. The investigator then walked away as he played out the line. When the gull returned, usually within a few minutes, and alighted on the nest, the fishing line was pulled thus tightening the noose around its legs.

In 1978 'walk-in' traps were also used. These are wire-mesh cages, approximately  $1 \times 1 \times 1.5$  m in dimensions, with a cone-shaped entrance projecting into the cage. A trail of popcorn was placed from the surrounding area into the cage. Gulls followed the bait into the trap readily, and once inside appeared unable to locate the small inner entrance and were thus trapped. This technique was particularly useful during the pre- and post-nesting phases of the cycle and also for capture of unmated or non-nesting birds. These traps occasionally caught both members of a pair simultaneously.

During the winter months, gulls were shot over the open ocean about 1 to 5 km off Dana Point, California, in December 1977 and February 1978.

**Procurement of blood samples.** Blood samples (2 to 10 ml) were collected from a wing vein into heparinized syringes within 3 to 30 min of capture. Each bird was then ringed with a numbered U.S. Fish and Wildlife Service aluminium ring plus a unique combination of colour rings for future identification in the field. Unilateral laparotomy was performed for identification of sex and assessment of gonadal development, and in females to assess the state of development of the oviduct. The length and width of testes were estimated, as were the diameters of the largest ovarian follicle and oviduct. Atretic and post-ovulatory follicles were also noted. These data provide an indication of stage in the reproductive cycle; they are not intended to provide an accurate description of the cycle in gonadal size. The birds were then released for subsequent observation and recapture.

Blood samples were centrifuged using a gasoline-driven generator as a source of power. Plasma samples were stored frozen in a portable liquid-nitrogen refrigerator. The refrigerator, which held approximately 35 litres of liquid nitrogen, could maintain samples frozen for up to 65 days. At the end of the season the refrigerator containing the samples was transported to the mainland and the samples transferred to dry ice for transport by air to Seattle where they were stored at  $-30$  C.

Blood samples from western gulls shot off Dana Point were obtained within 5 min via heart puncture into heparinized syringes. Gonads were removed and measured. Blood samples were centrifuged on the Irvine campus of the University of California and the plasma samples, frozen on dry ice, were transported by air to Seattle.

**Assays of hormones.** Luteinizing hormone (LH): The post-precipitation double-antibody radioimmunoassay of Follett et al. (1972) was used with the modifications described by Follett et al. (1975). The assay utilizes an anti-chicken LH serum, raised in rabbits, and highly purified chicken LH for radioiodination and standard curves. For each plasma sample, 40- $\mu$ l aliquots were assayed in duplicate. If duplicates differed by more than 15%, samples were re-assayed.

The validity of use of the chicken LH assay for measurement of LH in the western gull was tested as follows: Anterior pituitary glands from both males and females were homogenized in assay buffer and the LH content measured in triplicate at several dilutions. LH levels were also measured in triplicate at several dilutions of a single plasma pool from western gulls. In all cases the dilution curves were parallel with the standard curve for chicken LH, suggesting that LH from western gulls binds to the antiserum in a manner similar to that from the domestic fowl.

To assess interassay variation, the plasma pool was assayed in triplicate at three dilutions in each assay. The interassay variation for LH among the samples taken in 1977 and 1978 combined was 13.1%. Plasma levels of LH are expressed as ng/ml immunoreactive LH (irLH).

**Steroid hormones.** Plasma levels of progesterone,  $17\beta$ -hydroxy- $5\alpha$ -androstane-3-one (DHT), testosterone, oestrone, and oestradiol were measured by radioimmunoassay (Wingfield & Farner 1975).

The accuracy and plasma blanks for the steroid assay system for western gull plasma were determined as follows. Aliquots of a single plasma pool were treated with dextran-coated charcoal to remove endogenous steroids. After centrifugation the supernatant contains an essentially steroid-free plasma that was then divided into three parts and taken through the entire assay procedure in triplicate following addition of 0, 250, or 500 pg of each steroid hormone. Results are presented in Table I along with interassay variation and solvent blanks. Plasma levels of progesterone and androgens

are expressed as ng/ml; and oestrogens as pg/ml. A preliminary analysis of changes in hormone levels during the period of sampling revealed that there is a decrease in plasma LH and steroid hormones 30 to 60 min after capture. In this communication we present data from samples collected 3 to 30 min after capture. There is no well-defined change in plasma hormone levels during the day (see also Wingfield & Farner 1978a); for the most part, our samples were collected in the afternoon. The method of capture and sampling also had no apparent effect on circulating hormone levels.

**Field observations.** An analysis of several years of behavioural observations on pairs of western

**Table I. Solvent Blanks, Accuracy and Interassay Variation of Steroid-hormone Radioimmunoassays**

Hormone-assay system	Solvent* blank (pg)	Interassay† variation (%)
Dihydrotestosterone	< 2	22.2
Testosterone	< 2	14.8
Corticosterone	< 10	12.3
Oestrone	< 4	12.3
Oestradiol	< 4	13.9
Progesterone	< 4	20.0

	Amount of steroid hormone added (pg)‡	Amount of steroid hormone measured (pg)‡
Dihydrotestosterone	0	< 40
	250	234 ± 12
	500	533 ± 44
Testosterone	0	< 40
	250	303 ± 19
	500	552 ± 8
Corticosterone	0	< 50
	250	295 ± 26
	500	504 ± 63
Oestrone	0	< 10
	250	266 ± 6
	500	543 ± 22
Oestradiol	0	< 40
	250	249 ± 18
	500	474 ± 13
Progesterone	0	< 40
	250	255 ± 15
	500	559 ± 22

\*Amount of steroid hormone apparent from % bound in solvent blank.

†Expressed as coefficient of variation on a pool of plasma from western gulls.

‡Steroid added to a plasma pool from western gulls which was stripped of endogenous steroids.

gulls in specific areas of the colony on Santa Barbara Island is the subject of a separate communication (G. L. Hunt, Jr., A. L. Newman, M. H. Warner, J. C. Wingfield & J. Kaiwi, unpublished data). The following additional behavioural observations were made because individual colour-ring codes allowed us to identify the mate, if any, and where the nest, if any, was located. In 1977 daily censuses were taken of colour-ringed birds in the colony and observations were made on their reproductive status and stage in the cycle. The 'loafing areas' ('clubs', see Tinbergen 1953) were also observed. In 1978 such observations were made thrice daily 2 to 3 times per week. In addition, 2-h periods of observation were made 5 to 10 times per week from hides in specific areas of the colony. About eight pairs could be observed at each hide; in two of the areas, more than 80% of the birds were colour-ringed. Thus we were able to identify the sex of mates, and determine the date of egg laying and hatching.

Nests were also located over a major part of the colony. Each was marked with a numbered stake and regular inspections on its progress were made. Particular attention was paid to the nests of colour-ringed birds.

We were thus able to assign reproductive status on the basis of behavioural as well as physiological criteria to many of the colour-ringed birds. In addition, mates could be identified and nesting success could be determined in many cases.

In 1978 we made regular censuses, recorded reproductive status and collected blood samples from colour-ringed, unpaired individuals for which we had determined sex by earlier laparotomy.

Unpaired birds, almost always females, were placed in one of two categories (G. L. Hunt, Jr., A. L. Newman, M. H. Warner, J. C. Wingfield & J. Kaiwi, unpublished data). The first category includes unpaired females that often defended a temporarily vacant territory, but were always supplanted when the paired owners returned. Because the territory defended was not fixed, we refer to these females as 'floaters'. The second category of unmated females we have designated as 'non-breeders' since they were seen on the 'club' areas and were not observed to display any territorial behaviour. Some females in the second category may, however, display territorial behaviour in other colonies not observed by us.

**Statistics.** Data on hormone levels were subjected to an analysis of variance and levels of

significance determined by the Newman-Keuls multiple-range test for unequal samples. Comparisons between sexes were made with the Student's *t*-test.

### Results

Changes in size of gonads and in plasma levels of irLH and steroid hormones in heterosexually paired western gulls during the breeding season of 1977 are summarized in Fig. 1. Similar data for males and females of heterosexual pairs during the breeding season of 1978 are presented in Fig. 2 and Fig. 3, respectively. Because of incomplete synchrony of the breeding cycles among the pairs, the data are arranged according to the stage in the cycle rather than by calendar time (see Tables II-IV for explanation) and are spaced according to the mean time for a single pair to complete the cycle successfully.

Changes in plasma levels of irLH, DHT and testosterone were slight in both males and females with the highest concentrations occurring during, or just prior to, egg-laying in May. In females, these levels decreased to a minimum in the early stages of incubation ( $P < 0.05$ ). In males, testosterone levels also apparently decreased during the very early stages of incubation ( $0.05 < P < 0.1$ , Fig. 1;  $P < 0.01$ , Fig. 2), whereas levels of irLH reached a minimum only late in the parental phase ( $P < 0.05$ ). Plasma levels of both oestrone and oestradiol in females attained maxima coincident with yolk deposition and egg laying in 1977 (Fig. 1,  $P < 0.01$ ), but not in 1978 (Fig. 3) when, apparently because of poor trophic conditions, only 10 to 15 of the nesting females laid eggs. No significant changes in circulating oestrone and oestradiol were detected in males in either 1977 or 1978; in 1978 there were no statistically significant differences between males and females in the levels of these hormones.

Changes in diameter of ovarian follicles, plasma levels of irLH and steroid hormones of homosexually paired female western gulls are presented in Fig. 4. (See Table V for explanation of this figure.) We found no major differences between homosexually and heterosexually paired females in either the concentrations of hormones in the plasma or in their temporal patterns during the breeding season, with the exception of the period of incubation in which circulating irLH continued to increase in homosexually paired females (Fig. 4,  $P < 0.01$ ) and to decrease in heterosexually paired females (Figs 1 and 3).

The absolute levels of DHT and testosterone were virtually identical throughout most of the year among males and both heterosexually and homosexually paired females (Figs 1-4). The ratio of testosterone in the plasma of males to that of females barely exceeds 2.0 and then only for a very brief period during the egg-laying period of 1978 (Figs 2 and 3,  $P < 0.05$ ).

Plasma levels of progesterone were elevated during the period of ovulation and oviposition in heterosexually paired females in 1977 (Fig. 1,  $P < 0.05$ ) and also in homosexually paired females (Fig. 4,  $P < 0.01$ ). These levels declined as incubation progressed ( $P < 0.01$  in both cases). In heterosexually paired females in 1978, maximum levels occurred about one month before ovulation (Fig. 3,  $P < 0.05$ ), with levels becoming lower during egg laying. In males in 1978 progesterone levels did not change throughout the breeding period except for a possible decline at about the time of hatching of the eggs (Fig. 2,  $P < 0.05$ ). In contrast, in 1977 levels declined as the season progressed (Fig. 2,  $P < 0.01$ ).

In December 1977 and February 1978 plasma levels of irLH and DHT in both males and females were similar to those of the breeding period. Only during the period of egg laying in 1978 were plasma levels of testosterone in males higher than those recorded in December and February ( $P < 0.01$ , Fig. 2). However, these winter levels were not lower than those measured in males during the breeding season of 1977.

In Table VI we present plasma levels of LH, DHT, and testosterone in 'floaters' and 'non-breeders' from March through June. By May the 'floaters' were either paired or were spending much time in 'clubs' that consisted mainly of resting birds. Thus only non-breeders were observed from this time on. There were no differences in plasma levels of LH and androgens between floaters and non-breeders and, furthermore, these levels were not significantly different from paired females.

### Discussion

We can conclude that homosexual pairing of western gulls involves neither alteration of the circulating levels or temporal patterns of LH or androgens. Since there are no major differences in behaviour between females of homosexual and those of heterosexual pairs, little sexual dimorphism in most behaviours (G. L. Hunt, Jr., A. L. Newman, M. H. Warner, J. C. Wingfield

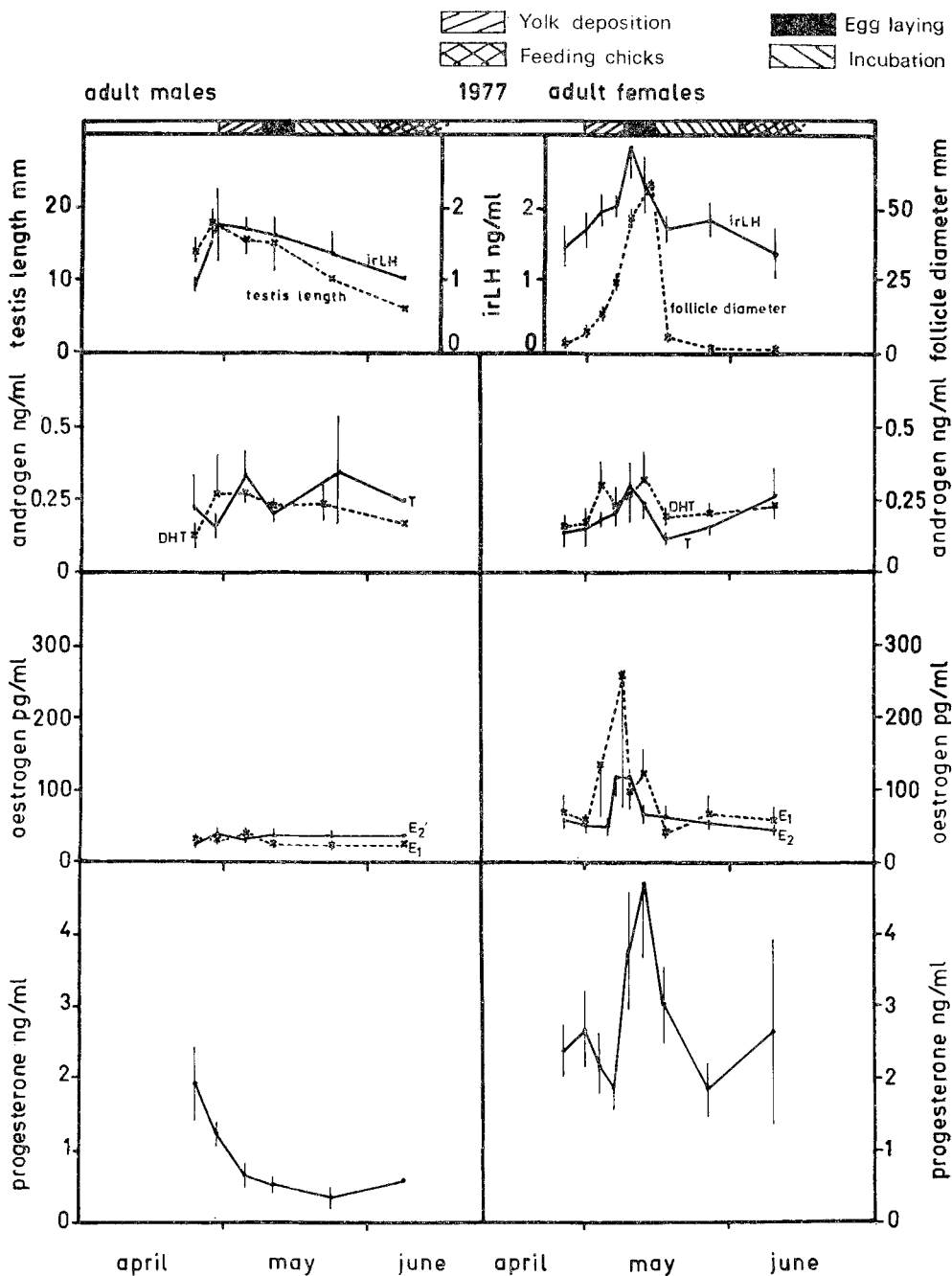


Fig. 1. Changes in length of testis, diameter of ovarian follicles and plasma levels of hormones in adult male and female western gulls, *Larus occidentalis wymani*, during the breeding season on Santa Barbara Island in 1977. See Table II for explanation of reduction of data. Stages in the reproductive cycle are indicated at the top of the figure. The cross hatched bar, up from left to right, represents the period of yolk deposition; solid bar, the period of egg laying; cross hatching, down from left to right, incubation period; and the double hatching, the period during which chicks are being fed. Vertical bars are standard errors of means.

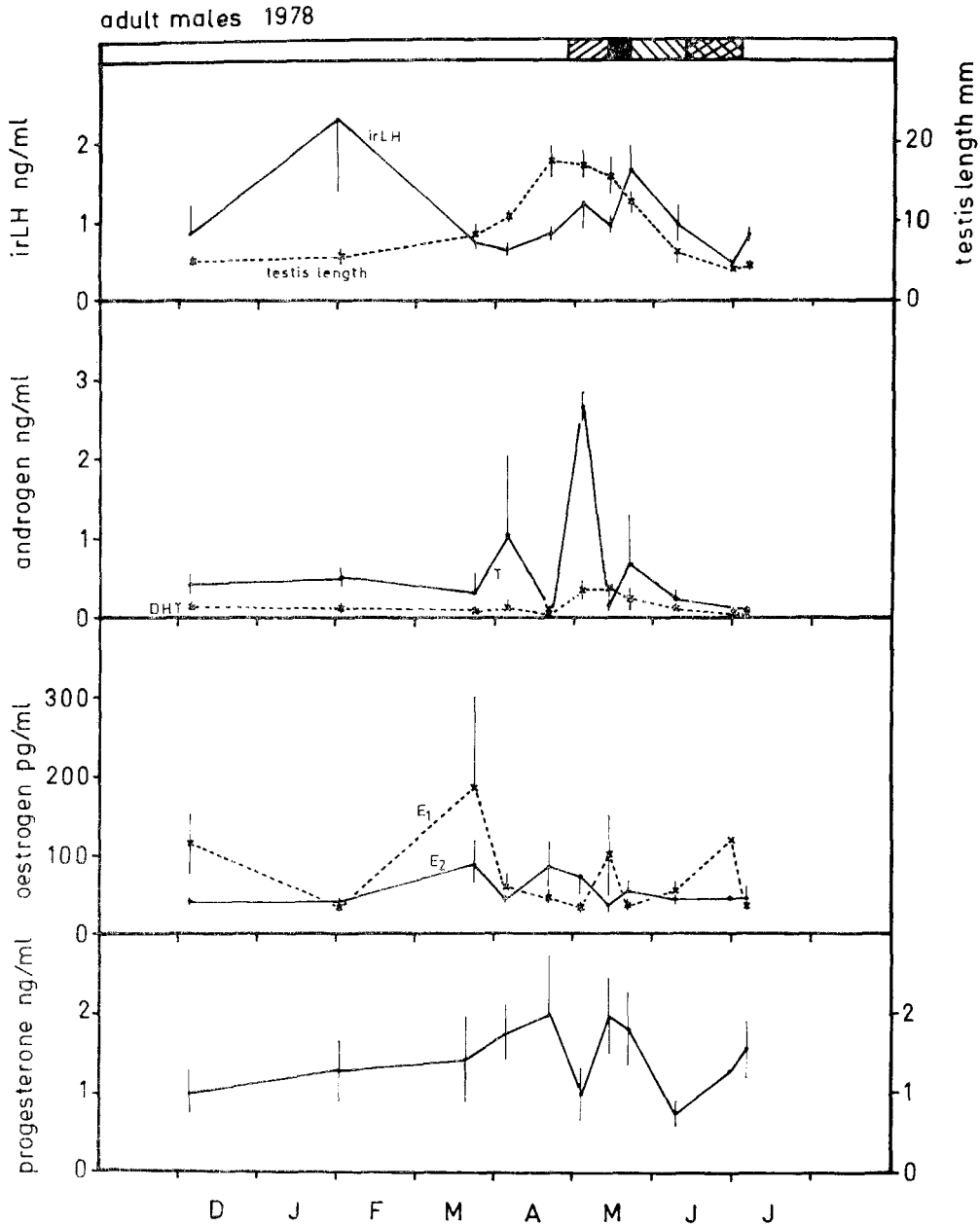


Fig. 2. Changes in length of testis and plasma levels of hormones in male western gulls, *Larus occidentalis wymani*, during the breeding season on Santa Barbara Island in 1978. See Table III for explanation of reduction of data. Stages in the reproductive cycle are indicated at the top of the figure: see Fig. 1 for key. Vertical bars are standard errors of means.

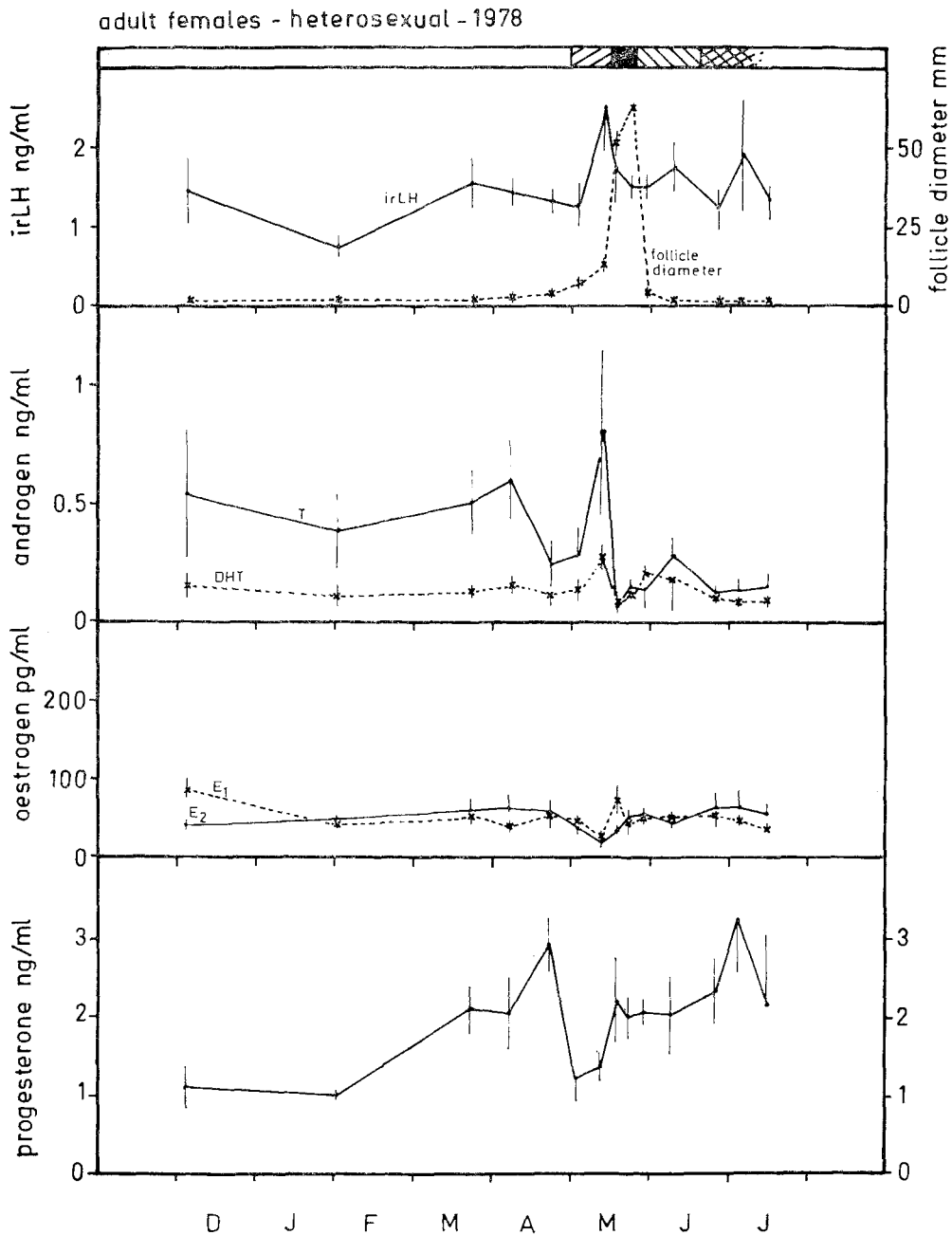


Fig. 3. Changes in diameter of ovarian follicles and plasma levels of hormones in heterosexually paired adult female western gulls, *Larus occidentalis wymani*, during the breeding season on Santa Barbara Island in 1978. See Table IV for explanation of reduction of data. Stages in the reproductive cycle are indicated at the top of the figure: see Fig. 1 for key. Vertical bars are standard errors of means.



& J. Kaiwi, unpublished data), and an apparent excess of females in the breeding population (Hunt et al. 1980), it is not difficult to rationalize the formation of female-female pairs. Since un-

paired adult females also have high levels of circulating androgen and may establish territories, a possible basis for the formation of female-female pairs is apparent.

Table II. Stages in the Breeding Cycle of Male and Female Western Gulls *Larus occidentalis wymani*, on Santa Barbara Island in 1977

	Description	Dates*	Sample size†
Male stages			
1	Territorial and paired, courtship behaviour	22-23 April	5-7
2	Courtship behaviour more marked, some copulations	24-30 April	7-9
3	Females undergoing yolk deposition, copulations	1-5 May	4-7
4	Ovulation and oviposition	5 May	4
5	Incubation	25 May-5 June	6
6	Feeding chicks	10 June	2
Female stages			
1	Territorial, paired, courtship behaviour, no yolk deposition	22 April-3 May	9-10
2	Yolk deposition, final maturation of follicles, courtship	22 April-5 May	5-6
3	Yolk deposition, courtship feeding	26 April-3 May	3-4
4	Yolk deposition, copulations seen	26 April-5 May	4-5
5	About to ovulate	26 April-24 May	5-7
6	Egg in oviduct	26 April-24 May	8-9
7	Early incubation	5-21 May	9
8	Late incubation	18 May-6 June	7-8
9	Feeding chicks	9-10 June	3

\*Dates represent the period in which birds in this stage of the cycle were captured. These dates do not necessarily represent the period for the population as a whole.

†Sample sizes vary as plasma volumes obtained from some birds were insufficient for determination of all hormone levels.

Table III. Stages in the Breeding Cycle of Male Western Gulls, *Larus occidentalis wymani*, on Santa Barbara Island in 1978

Stage	Description	Dates*	Sample size†
1	Collected on open ocean off Dana Point	5-7 December	5
2	Collected on open ocean off Dana Point	2 February	6-9
3	Territorial and paired on Santa Barbara Island; gonadal growth underway	19-31 March	5
4	Gonadal growth nearing completion, courtship and territorial behaviour	1-15 April	4
5	Gonadal growth complete, courtship, territorial behaviour, some nest building	16-30 April	4
6	Females showing yolk deposition, nest building	3-23 May	3
7	Females ovulating	12-14 May	3
8	Early incubation	7-27 May	4
9	Late incubation	21 May-23 June	4
10	Feeding chicks	6 July	1
11	Post-breeding	26 June-13 July	7

\*Dates represent the period in which birds in this stage of the cycle were captured. These dates do not necessarily represent the period for the population as a whole.

†Sample sizes vary as plasma volumes obtained from some birds were insufficient for the determination of all hormone levels.

It is of particular interest that we have found the circulating levels of DHT and testosterone in plasma to be virtually identical throughout most of the year among breeding males, and hetero- and homosexually paired females (Figs 1-4). The ratio of androgen in male plasma to that in the female exceeds 2.0 only slightly, and then only during the egg-laying period of 1978 (Figs 2 and 3). In contrast, in the white-crowned sparrow, *Zonotrichia leucophrys* (Wingfield & Farner 1977; 1978a, b), ring dove (Feder et al. 1977) and mallard, *Anas platyrhynchos* (Donham 1980), and other species, this ratio may be between 4 and 20 (Table VII).

These specific differences in male-female androgen ratios may be related to differences in the degree of sexual dimorphism in reproductive behaviour and plumage. The male white-crowned sparrow is the primary defender of territory. He does not incubate eggs but does feed young. Furthermore, there are well defined dimorphisms in sexual behaviours in this species (J. C. Wingfield, M. C. Moore & D. S. Farner, unpublished data). In ring doves there is a well documented dimorphism in sexual behaviour in which the male performs the 'bow-coo' display, although males and females share incubation and feeding of young (Silver 1978; Cheng 1979). Unlike the white-crowned sparrow and ring dove,

there is a marked dimorphism in plumage in the mallard, a species in which the male plays no part in incubation or care of the young (e.g. Donham 1980). In the western gull there is no sexual dimorphism in plumage; territorial defence and parental duties are more or less equally divided between the members of the pair (Wingfield et al. 1980a). Quantified observations on behaviour of western gulls on Santa Barbara Island demonstrate that males defend territory more than females, but the differences between the sexes are less when the mate is absent (G. L. Hunt, Jr., A. L. Newman, M. H. Warner, J. C. Wingfield & J. Kaiwi, unpublished data), and that at least some females are capable of establishing their own territories. Furthermore there are few differences in sexual behaviour between males and females. Males do mount more and courtship feed somewhat more than females, although the latter have been observed to mount other females and, on occasion, males. Females do more head tossing than males.

As in other avian groups, breeding plumage and reproductive behaviour of gulls appear to be under the control of androgens. Castrated male black-headed gulls (*Larus ridibundus*) fail to develop adult colour of legs, bill, and plumage (van Oordt & Junge 1930). When fragments of testicular tissue were implanted into castrated

Table IV. Stages in the Breeding Cycle of Heterosexually Paired Female Western Gulls, *Larus occidentalis wymani*, on Santa Barbara Island in 1978

Stages	Description	Dates*	Sample sizes†
1	Collected on open ocean off Dana Point	5-7 December	8-10
2	Collected on open ocean off Dana Point	2 February	4-5
3	Territorial and paired on Santa Barbara Island; no yolk deposition	19-31 March	12
4	Yolk deposition beginning, courtship and territorial behaviour	1-15 April	10
5	Yolk deposition beginning, courtship and territorial behaviour	16 April-1 May	11
6	Yolk deposition, courtship and territorial behaviour, some nest building	25 April-16 May	7
7	Yolk deposition, copulation, nest building	9-14 May	3
8	About to ovulate	9-26 May	4-5
9	Egg in oviduct	7 May-9 June	17
10	Early incubation	13-27 May	10
11	Late incubation	24 May-22 June	7
12	Feeding chicks	9 June-11 July	9
13	Post-breeding	26 June-5 July	5

\*Dates represent the period in which birds in this stage of the cycle were captured. These dates do not necessarily represent the period for the population as a whole.

†Sample sizes vary as plasma volumes obtained from some birds were insufficient for the determination of all hormone levels.

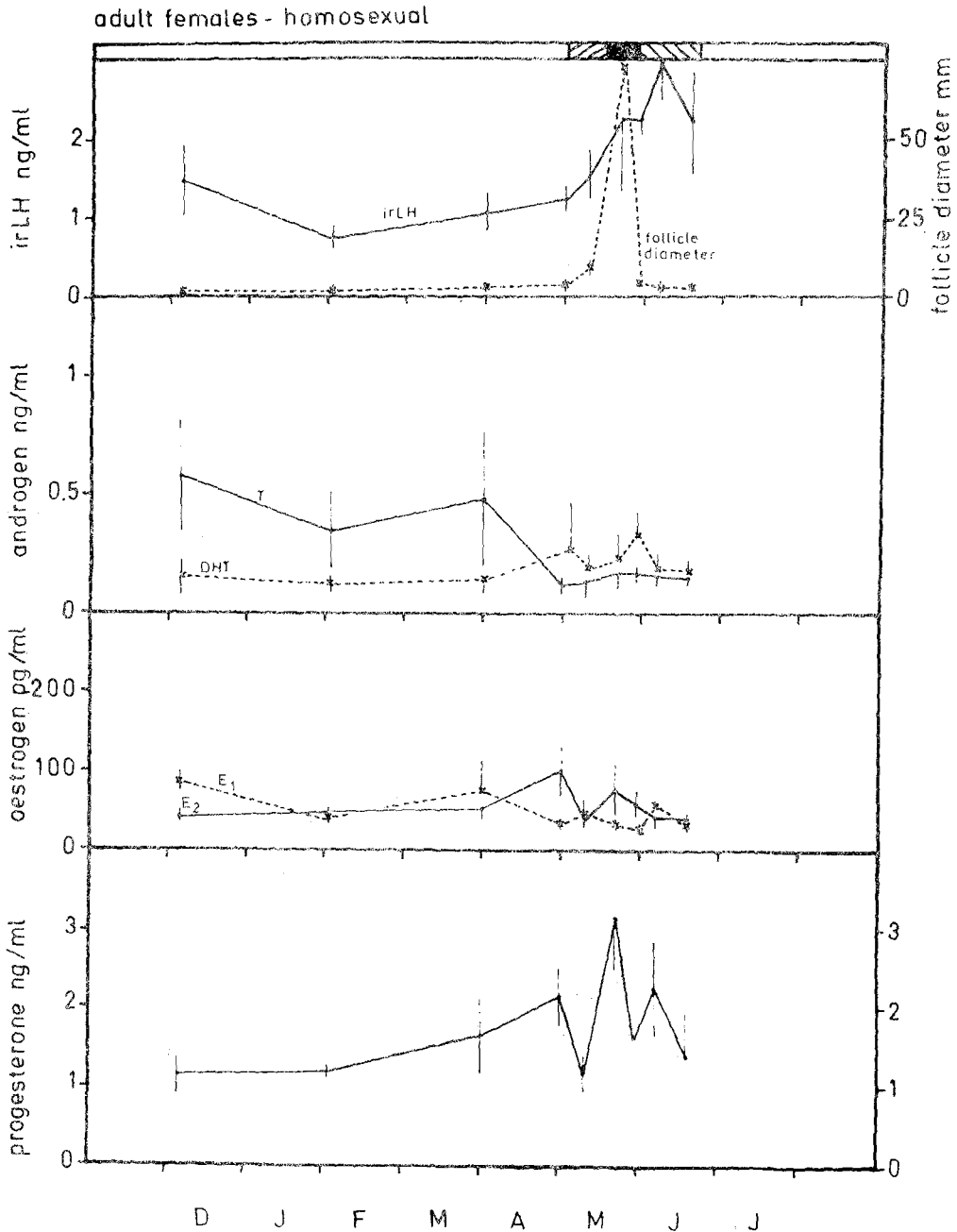


Fig. 4. Changes in diameter of ovarian follicles and plasma levels of hormones in homosexually paired adult female western gulls, *Larus occidentalis wymani*, during the breeding season on Santa Barbara Island in 1977 and 1978. See Table V for explanation of reduction of data. Stages in the reproductive cycle are indicated at the top of the figure: see Fig. 1 for key. Vertical bars are standard errors of means.

gulls, the normal summer plumage developed in spring (van Oordt & Junge 1933). Gonadectomized laughing gulls (*L. atricilla*) also fail to develop adult colour of head feathers, eye rings and legs during the breeding season. But injection of testosterone propionate induces these changes in gonadectomized birds of both sexes whereas oestradiol is without effect (Noble & Wurm 1940). Injection of testosterone also induces vocalizations and postures common to both sexes whereas the effects of injection of oestradiol appear to be restricted to induction of characteristic sexual behaviour of females (Terkel et al. 1976). Similarly in the herring gull (*L. argentatus*) injections of androgen into immature birds of both sexes induce premature develop-

ment of adult beak colour and plumage as well as increased aggressiveness, territorial behaviour and adult vocalizations, although this treatment is less effective in females; oestradiol was found to be without effect (Boss 1943).

The similarity in levels of the two androgens measured in male and female western gulls does not, of course, preclude the possibility of other differences in male sex hormones, such as the secretion of androstenedione or other androgens. Furthermore, it is possible, indeed probable, that there are differences in numbers and sites of androgen receptors. Also not to be precluded are possible effects of aromatization of testosterone to oestradiol in non-ovarian tissues (e.g. Callard et al. 1978).

Table V. Stages in the Breeding Cycle of Homosexually Paired Female Western Gulls, *Larus occidentalis wymani* (data for 1977 and 1978 combined)

Stage	Description	Dates*	Sample sizes†
1	As for Table IV		
2	As for Table IV		
3	Territorial and paired on Santa Barbara Island, no yolk deposition	28 March–16 April	4
4	Territorial and paired, no yolk deposition	17 April–20 May	4
5	Yolk deposition, courtship and territorial behaviour	7–20 May	4
6	Egg laying	14–28 May	3
7	Early incubation	19–27 May	11
8	Mid-incubation	22–31 May	6
9	Late incubation	27 May–6 June	3–5

\*Dates represent the period in which birds in this stage of the cycle were captured. These dates do not necessarily represent the period for the population as a whole.

†Sample sizes vary as plasma volumes obtained from some birds were insufficient for the determination of all hormone levels.

Table VI. Plasma Levels of Luteinizing Hormone (LH), Dihydrotestosterone (DHT), and Testosterone (T) in 'Floating' and Non-breeding Female Western Gulls, *Larus occidentalis wymani*, on Santa Barbara Island in 1978

	March		April		May	June–July
	F*	NB†	F	NB	NB	NB
<i>N</i>	7	6	5	12	5	8
LH ng/ml	1.57 ± 0.17	0.99 ± 0.17	1.15 ± 0.25	1.35 ± 0.12	2.21 ± 1.10	1.62 ± 0.23
DHT pg/ml	120 ± 99	211 ± 131	276 ± 121	197 ± 43	179 ± 117	364 ± 124
T pg/ml	318 ± 98	214 ± 131	413 ± 192	408 ± 171	175 ± 65	136 ± 42

\*'Floaters'.

†Non-breeders.

Means ± standard errors.

A second interesting physiological feature of reproduction in the western gull is the lack of marked seasonal cycles in plasma levels of LH, DHT, and testosterone, despite marked changes in gonadal size and behaviour. Testes are at maximum size and ovarian follicles at maximum diameter in late April or May (Figs 1-4). The magnitude of these changes is similar to those observed in the common gull, *L. canus* (Thybusch 1965) and in the California gull, *L. californicus* (Johnston 1956a, b). Seasonal changes in plasma levels of LH in western gulls are slight, although there is a tendency for higher levels just prior to the egg-laying period. This low-amplitude cycle in western gulls contrasts conspicuously with the 10- to 100-fold differences in the concentrations of LH measured over the course of a year in the blood of *L. argentatus* (Scanes et al. 1974) and other species (cf. Wingfield & Farner 1980). However, a low-amplitude annual cycle of plasma LH similar to that of western gulls has also been reported in the South African Cape cormorant, *Phalacrocorax capensis* (Berry et al. 1979).

It is curious that plasma levels of LH in western gulls continue to increase during incubation in homosexually paired western gulls, whereas they decrease in heterosexually paired females (Figs 1, 3 and 4); we are unable at this time to offer an explanation for this phenomenon.

The low amplitude of the seasonal changes in circulating levels of DHT and testosterone may be similar to those of the California gull and the northern fulmar (*Fulmaris glacialis*), since in

these species the cells of Leydig are active from January to July (Marshall 1949; Johnston 1956a). This suggests relatively high winter levels of androgens as is the case in the western gull. However, another marine species, the Cape cormorant (*Phalacrocorax capensis*), maintains basic levels of testosterone throughout the non-breeding season (Berry et al. 1979), which is also the case with the lesser sheathbill, *Chionis minor*, even though some males display territorial behaviour throughout the year (Burger & Millar 1980). Elevated levels of LH and/or androgens in the plasma during autumn and early winter have been noted in a number of species (e.g. Lincoln et al. 1980) and appear to be related to an increase in sexual and territorial behaviour, although breeding rarely, if ever, occurs at that time. The western gulls of southern California are sedentary, with many individuals remaining in the vicinity of the Channel Islands throughout the year. Also, although they appear not to visit their breeding territories from August to early December, territorial birds are frequent on Santa Barbara Island from December through July. Thus, even though seasonal changes in androgen levels are relatively small, the period of territorial behaviour of the western gull correlates very well with the period of highest circulating levels of androgens.

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Table VII. Comparison of Plasma Levels of Androgens Among Species with Differing Levels of Sexual Dimorphism

Species	Level of sexual dimorphism		Ratio androgens $\delta/\text{♀}^*$
	External morphological differences	Behavioural	Testosterone
<i>Zonotrichia leucophrys</i>	slight	great	10-20
<i>Anas platyrhynchos</i>	great	great	10-20
<i>Turdus merula</i>	great	great	10-20
<i>Sturnella neglecta</i>	slight	great	5-10
<i>Poocetes gramineus</i>	slight	great	5
<i>Streptopelia risoria</i> †	none	great	3-5
<i>Larus occidentalis wymani</i>	slight	slight	1-2

\*Breeding season.

†Domesticated ring-dove

Compiled from Donham (1980), Feder et al. (1977), Wingfield & Farner (1977, 1978a,b, 1980 and unpublished data), H. Schwabl, J. C. Wingfield, E. Gwinner and D. S. Farner (unpublished data).

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