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## Research

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### Author for correspondence:

Lindsay C. Young

e-mail: [lindsay@pacificrimconservation.com](mailto:lindsay@pacificrimconservation.com)

# Adaptive value of same-sex pairing in Laysan albatross

Lindsay C. Young and Eric A. VanderWerf

Pacific Rim Conservation, PO Box 61827, Honolulu, HI 96839, USA

Same-sex pairing is widespread among animals but is difficult to explain in an evolutionary context because it does not result in reproduction, and thus same-sex behaviour often is viewed as maladaptive. Here, we compare survival, fecundity and transition probabilities of female Laysan albatross in different pair types, and we show how female–female pairing could be an adaptive alternative mating strategy, albeit one that resulted in lower fitness than male–female pairing. Females in same-sex pairs produced 80% fewer chicks, had lower survival and skipped breeding more often than those in male–female pairs. Females in same-sex pairs that raised a chick sometimes acquired a male mate in the following year, but females in failed same-sex pairs never did, suggesting that males exert sexual selection by assessing female quality and relegating low-quality females into same-sex pairs. Sexual selection by males in a monomorphic, non-ornamented species is rare and suggests that reconsideration is needed of the circumstances in which alternative reproductive behaviour evolves. Given the lack of males and obligate biparental care in this species, this research demonstrates how same-sex pairing was better than not breeding and highlights how it could be an adaptive strategy under certain demographic conditions.

## 1. Introduction

Same-sex pairing behaviour is widespread among animal species, but is difficult to explain in an evolutionary context because it cannot directly result in reproduction [1–3]. In addition, many reported instances of such behaviour occur in captivity, are associated with unusual environmental conditions, or are anecdotal, further hampering meaningful interpretation of the adaptive value [1]. In some cases, same-sex behaviour confers an advantage, for example in primates where same-sex behaviour may function as a social currency during conspecific encounters [4]. In other cases, the behaviour incurs costs: female sand beetles spend most of their life physically resisting mating attempts by males as a result of the high cost of mating [5,6] and researchers have been thus far unable to find evidence of an adaptive benefit to it. Some same-sex behaviour has even been attributed to mating errors [7] or animals ‘practising’ mating [8]. Without consistencies in the function of same-sex behaviour across taxa, investigations into the adaptive function of same-sex behaviour have been done on a taxon-by-taxon basis, and as a result same-sex behaviour has often been dismissed as maladaptive, as few opportunities exist to study it in wild populations.

In a recently established Laysan albatross (*Phoebastria immutabilis*) colony on the island of Oahu, HI, USA, 31% of breeding pairs consist of two unrelated females that cooperate to raise a chick [9]. The egg is laid by one member of the pair (females appear to alternate whose egg is incubated each year) and fathered by an already-paired male in the colony. The sex ratio in this colony is 60% female as a result of female-biased immigration, and the skewed sex ratio is thought to be causing the high prevalence of same-sex pairing [9]. Sex ratio skews can have a large impact on breeding systems that partition parental care between the sexes [10] and sex roles can change as a result [11–13]. Biases in adult sex ratios are common in birds [14], but skews typically are male-biased owing to higher female mortality [10]. Likewise, alternative reproductive strategies are often employed by males because females are typically the ‘choosy’ sex because of their higher physiological investment in offspring [15]. In the case of Laysan

**Table 1.** Five-state models used to investigate annual survival ( $\varphi$ ), encounter probability ( $p$ ) and transition probabilities ( $\psi$ ) among female Laysan albatrosses in male–female pairs that fledged a chick (A), male–female pairs that failed to raise a chick (B), female–female pairs that raised a chick (C), female–female pairs that failed to raise a chick (D), and that skipped breeding (S), at Kaena Point, Oahu. (Subscripts indicate whether parameters were constant across all states, indicated by a dot (.), or differed among certain states, with states that differed separated in parentheses. For example,  $\varphi_{(AC)(BDS)}$  indicates that survival varied among states, with states A and C being similar to each other and different from states B, D and S, and vice versa.)

model no.	model parameters	$\Delta AIC_c$	model likelihood	num. par.
1	$\varphi_{(AC)(BDS)} p. \psi_{A(B)(CD)(S)} \psi_{B(A)(CD)(S)} \psi_{C(AB)(D)(S)} \psi_{D(AB)(C)(S)} \psi_{S(AB)(CD)}$	0	1.00	17
2	$\varphi. p. \psi_{A(B)(CD)(S)} \psi_{B(A)(CD)(S)} \psi_{C(AB)(D)(S)} \psi_{D(AB)(C)(S)} \psi_{S(AB)(CD)}$	0.80	0.67	16
3	$\varphi. p. \psi_{A(B)(CD)(S)} \psi_{B(A)(CD)(S)} \psi_{C(AB)(D)(S)} \psi_{D(AB)(C)(S)} \psi_{S.}$	0.97	0.62	15
4	$\varphi_{(A)(C)(BDS)} p. \psi_{A(B)(CD)(S)} \psi_{B(A)(CD)(S)} \psi_{C(AB)(D)(S)} \psi_{D(AB)(C)(S)} \psi_{S(AB)(CD)}$	1.91	0.38	18
5	$\varphi. p. \psi_{A(B)(CD)(S)} \psi_{B(A)(CD)(S)} \psi_{C(AB)(D)(S)} \psi_{D.} \psi_{S.}$	91.06	0	13
6	$\varphi. p. \psi_{A(B)(CD)(S)} \psi_{B(A)(CD)(S)} \psi_{C.} \psi_{D.} \psi_{S.}$	128.00	0	11
7	$\varphi. p. \psi_{A(B)(CD)(S)} \psi_{B.} \psi_{C.} \psi_{D.} \psi_{S.}$	258.04	0	9
8	$\varphi. p. \psi_{A.} \psi_{B.} \psi_{C.} \psi_{D.} \psi_{S.}$	391.19	0	7

albatross, however, these roles appear to have been reversed, and females, rather than males, may be ‘making the best of a bad job’, with those in female–female (FF) pairs achieving higher reproductive success than if they had simply not bred, albeit lower than that in male–female (MF) pairs.

Here, we investigate the adaptive value and evolutionary significance of same-sex pairing in a female-biased population of Laysan albatross by comparing survival, fecundity and the transition probabilities of females in different pair types.

## 2. Material and methods

We monitored Laysan albatrosses at Kaena Point Natural Area Reserve on Oahu, HI, USA from 2003 to 2012 following protocols in Young *et al.* [9,16] and VanderWerf & Young [17]. We marked each bird with a metal ring and a field-readable plastic ring to facilitate monitoring of birds without having to recapture them, and we collected a 400  $\mu$ l blood sample from the tarsal vein for genetic analysis. We monitored pairs daily during the courtship and egg-laying period, and then weekly for the remainder of the reproductive season.

We determined the sex of each bird genetically using standard techniques for non-ratite birds involving the chromohelicase DNA binding gene described by Fridolfsson & Ellegren [18] and Young *et al.* [9]. We extracted DNA using an ID Labs DNA isolation kit and sexed all individuals at least twice, and all putative female–female pairs were sexed four times to confirm results. We used birds that had been physically observed laying an egg as positive female controls during sexing analyses.

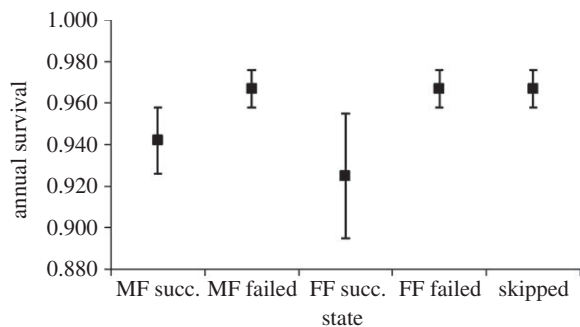
We considered individuals that shared incubation of an egg and feeding of a chick to be a pair. Albatross can only lay and incubate a single egg each year, so in FF pairs where both females sometimes laid an egg, only one egg was effectively incubated [9]. We defined reproductive success as the proportion of incubated eggs that resulted in a chick fledged, not counting the discarded eggs in cases where both females laid an egg. We compared annual reproductive success of FF and MF pairs with an ANOVA using the number of young fledged by each female as the dependent variable and pair type and year as independent variables. We also compared the fitness of individual females in FF and MF pairs during the 10-year study period using an ANOVA with the total number of chicks raised by each bird as the dependent variable and pair type as the independent variable. For females that switched pair types during the study ( $n = 17$ ), the reproduction was divided appropriately into each pair type by year.

To measure annual survival and shifts in pairing patterns, we created an encounter history for each female Laysan albatross that bred on Oahu from 2003 to 2012 ( $n = 145$ ), and categorized them using the sex of the bird’s mate and reproductive success each year. We used five-state models in program MARK v. 5.1 [19] to generate maximum-likelihood estimates of annual survival ( $\varphi$ ), detection probability ( $p$ ) and transition probability ( $\psi$ ) of females among different states: successful MF pair (A), failed MF pair (B), successful FF pair (C), failed FF pair (D) and skipped breeders (S) or birds that had bred before but skipped in a given year.

We began with the simplest model in which all parameters were constant across all states, then added parameters designed to test hypotheses about the states. In mark-recapture analyses, hypotheses are tested by comparing the fit of models that do versus do not contain a particular parameter [20]. We compared the fit of models with Akaike’s information criterion corrected for small sample sizes ( $AIC_c$ ), as calculated by program MARK. If the addition of a parameter resulted in improved fit, then the estimated values were judged to differ significantly between the states in question. The model with the lowest  $AIC_c$  value was considered to have the best fit. Models with  $AIC_c$  values that differed ( $\Delta AIC_c$ ) by less than or equal to 2.0 from the best model also were considered to have a reasonable fit and warrant some consideration [21]. Model notation follows Lebreton *et al.* [20], in which subscripts indicate whether parameters were constant across all states, indicated by a dot (.), or differed among certain states, with states that differed separated in parentheses. For example,  $\varphi_{(AC)(BDS)}$  indicates that survival varied among states, with states A and C being similar to each other and different from states B, D and S, and vice versa.

## 3. Results

FF pairs raised fewer offspring per year on average ( $0.26 \pm 0.04$ ) than MF pairs ( $0.66 \pm 0.02$ ;  $F_{1,8} = 75.6$ ,  $p < 0.001$ ). As each female in an FF pair was on average related to only half the offspring it raised [9], annual productivity of females in FF pairs actually was 80% lower than that in MF pairs. The total number of young raised by individual females over the 10-year study period was lower for females in FF pairs ( $1.00 \pm 0.12$ , range 0–4) than for females in MF pairs ( $2.17 \pm 0.18$ , range 0–7;  $F_{1,171} = 23.34$ ,  $p < 0.001$ ), demonstrating they had lower fitness during the 10-year study, which represents 20% of their reproductive lifespan. Again, as each female in an FF pair was on average related to only half the young it raised, their fitness



**Figure 1.** Annual survival rates of female Laysan albatrosses in different pair types based on the previous years' reproductive outcome. succ. indicates a successful reproductive attempt (chick fledged), failed is a dead egg or dead chick and skipped are birds that skipped breeding that year. Error bars are s.e.

was 77% lower than that of females in MF pairs. Females that switched pair types during the study were particularly instructive; the same birds raised fewer offspring while in FF pairs ( $1.06 \pm 0.16$ ) than in MF pairs ( $1.94 \pm 0.36$ ;  $F_{1,32} = 5.06$ ,  $p = 0.032$ ).

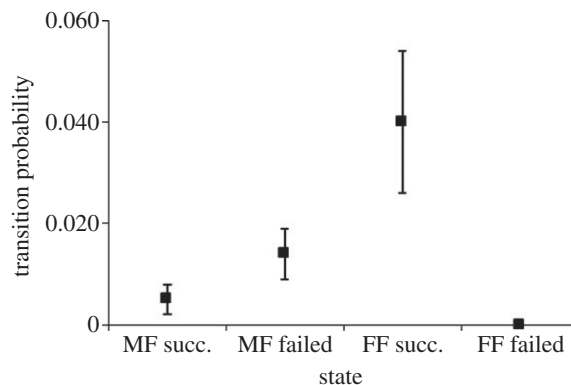
The best mark-recapture model included parameters that showed survival differed among some states and also that transitions from all five states were not constant (table 1, model 1). Annual survival was higher ( $0.967 \pm 0.009$ ) in states that failed to reproduce, including MF pairs, FF pairs and skipped breeders, than in successful breeders, indicating a cost to reproduction (figure 1). There was some evidence that survival was lower in successful FF pairs ( $0.925 \pm 0.030$ ) than in successful MF pairs ( $0.942 \pm 0.016$ ), but this difference was not as well supported (table 1, model 4).

For females in MF pairs, the chance of transitioning to an FF pair was low, but it was almost three times higher in MF pairs that failed in their breeding attempt (0.014) than in those that successfully raised a chick (0.005; figure 2). Conversely, for females in FF pairs, the chance of transitioning to an MF pair was relatively high in successful pairs (0.04), but zero in failed pairs. Females in failed FF pairs never acquired a male mate the next year even though unpaired males were present in the colony.

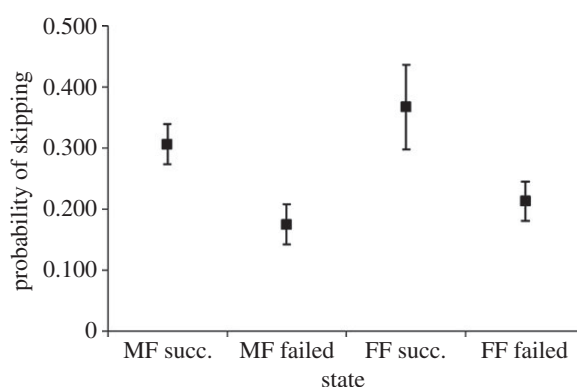
The probability of skipping breeding was higher following successful reproduction than after failure, for both FF ( $0.367 \pm 0.069$  versus  $0.213 \pm 0.032$ ) and MF pairs ( $0.306 \pm 0.033$  versus  $0.175 \pm 0.032$ ), and was higher in FF pairs (figure 3). The consequences of skipping were opposite for females in different pair types (figure 4). For females in unsuccessful FF pairs, skipping was an alternative way of obtaining a male mate without having fledged a chick. For females in successful MF pairs, skipping meant that they risked losing a male mate and being relegated to form an FF pair (figure 4).

## 4. Discussion

Females in FF pairs had lower fitness than females in MF pairs; they raised fewer offspring on average each year, and individual females in FF pairs produced fewer total offspring during the 10-year period of this study. These differences in reproductive output between the pair types would be magnified over the lifetime of the birds because females in FF pairs also appear to have lower survival, which would



**Figure 2.** Probability of female Laysan albatrosses transitioning to a different pair type based on the previous years' reproductive outcome. succ. indicates a successful reproductive attempt (chick fledged), and failed is a dead egg or dead chick. Error bars are s.e.

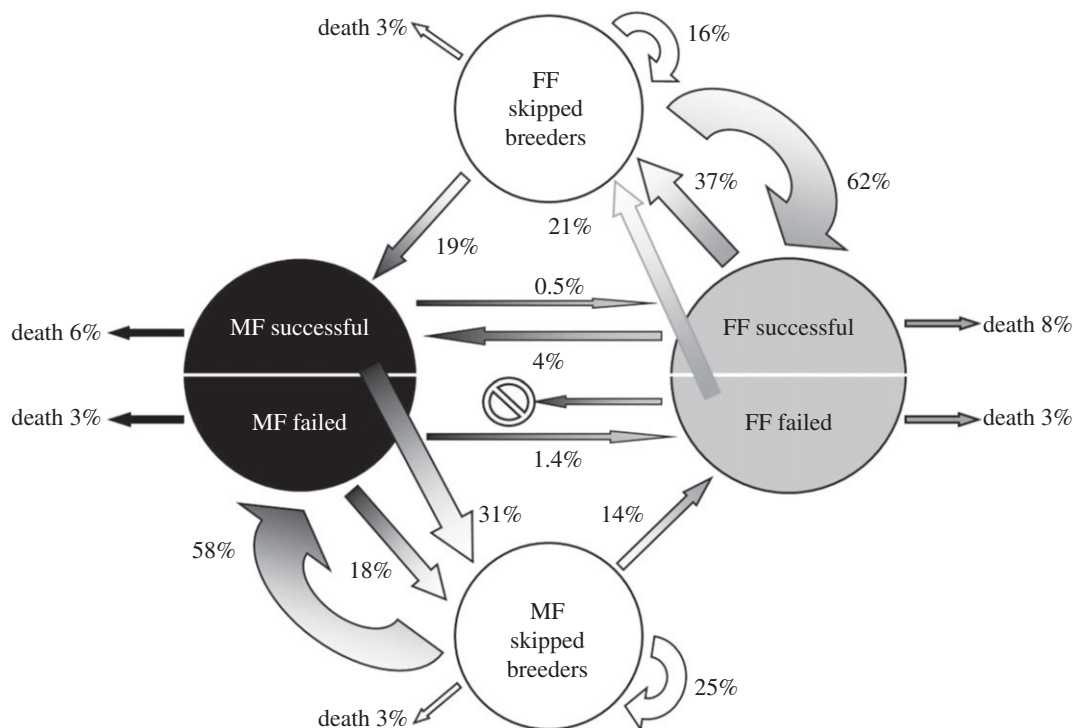


**Figure 3.** Probability of female Laysan albatrosses in a given pair type skipping breeding in the following year based on the previous years' reproductive outcome. succ. indicates a successful reproductive attempt (chick fledged), and failed is a dead egg or dead chick. Error bars are s.e.

probably further reduce their lifetime fitness compared with females in MF pairs.

The low survival of females in successful FF pairs presumably occurred because the female that took the first three-week incubation shift, which typically would be done by the male [22], and experienced greater nutritional stress because she just laid an egg but could not return to sea to feed. Although survival of females in failed FF pairs was high, it did not result in enhanced fitness because such birds did not reproduce. In order for a female in a failed FF pair to acquire a male mate, she had to breed successfully in an FF pair or skip a year of breeding and re-enter the pool of prospective mates (figure 4). This leads to the possibility that competition for male mates could manifest itself by females skipping less often in order to retain male mates even when they are in poor condition because birds skip breeding to improve body condition [23,24]. Other species have been shown to increase their reproductive effort with decreased access to males as a result of uncertainty in future reproductive attempts [25].

These results also suggest that male mate acquisition and retention are related to female reproductive performance and individual quality. This type of mate choice, whereby successful breeding in 1 year influences pair formation in the following year, has been observed in other species for opposite-sex pairs [26] but not in same-sex pairs and rarely in situations where males are the choosy sex [15]. If a female in a successful MF



**Figure 4.** Life stage transition probability and annual survival probability for female Laysan albatrosses in different pair types based on the previous years' reproductive outcome. Arrows indicate the direction of the transition and numbers are the rate of change. Successful indicates a successful reproductive attempt (chick fledged), failed is a dead egg or dead chick and skipped are birds that skipped breeding that year.

pair skipped the next breeding season, her survival rate would be 3% higher, but her chance of transitioning to an FF pair in the following year also was higher (14% versus 0.5%). So there was a survival benefit to skipping, but there also was a reproductive cost in terms of a missed breeding opportunity in the skipped year and in future years owing to lower mate retention and lower success in FF pairs.

If female Laysan albatrosses in FF pairs successfully reproduced, they could acquire a male mate, which increased annual fecundity, and probably, lifetime fitness. These results, coupled with the apparent availability of unpaired males on the colony, suggest that males are exerting sexual selection on females by choosing the highest quality females as mates and relegating lower quality females to pair with another female.

Female–female competition is observed most often when there is a skewed operational sex ratio that limits access to males or the opportunity to mate [27]. Sex-ratio theory indicates that the number or availability of potential mates can strongly influence evolutionary strategies as a result of this competition [28]. Alternative reproductive strategies, such as 'sneaker' and 'satellite' males, have been observed most often in males [29,30]; the occurrence of an alternative mate acquisition strategy in female Laysan albatrosses, skipping, suggests a broadening of the circumstances in which alternative reproductive behaviour evolves, particularly in a sexually monomorphic

species with internal fertilization and obligate biparental care. The consequences of demographic processes shaping mating systems is of increasing interest [27,31,32] and our results contribute some rare empirical data about the interactions among population dynamics, demography and social organization to the prevalence of a particular mating system.

Same-sex pairing appears to be part of a flexible breeding strategy that female Laysan albatrosses employ in response to dynamic social conditions, for example sex-ratio fluctuations. Compared with the option of not breeding at all, FF pairing may indeed be 'making the best of a bad job' in response to a shortage of males. The adaptive value, and the associated reversal of traditional gender roles in sexual selection, represent previously unconsidered correlates of same-sex behaviour in this species and highlight the need to determine the sex of each member of a pair in sexually monomorphic species.

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