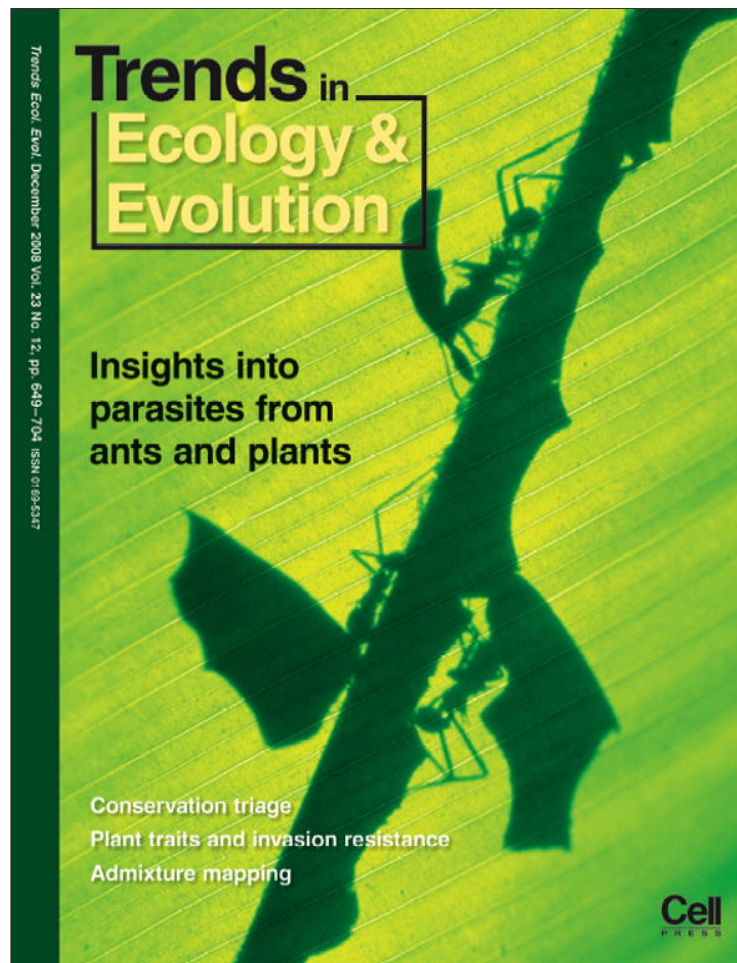


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- 8 McGraw, K.J. *et al.* (2004) European barn swallows use melanin pigments to color their feathers brown. *Behav. Ecol.* 15, 889–891
- 9 Safran, R.J. *et al.* (2005) Dynamic paternity allocation as a function of male plumage color in barn swallows. *Science* 309, 2210–2212
- 10 Wingfield, J.C. *et al.* (1990) The challenge hypothesis: theoretical implications for patterns of testosterone secretion, mating systems, and breeding strategies. *Am. Nat.* 136, 829–846
- 11 Tibbetts, E.A. and Dale, J. (2004) A socially enforced signal of quality in a paper wasp. *Nature* 432, 218–222
- 12 Husak, J.F. and Moore, I.T. (2008) Stress hormones and mate choice. *Trends Ecol. Evol.* 23, 532–534
- 13 Ducrest, A.-L. *et al.* (2008) Pleiotropy in the melanocortin system, coloration and behavioural syndromes. *Trends Ecol. Evol.* 23, 502–510
- 14 Price, T. (2008) *Speciation in Birds*. Roberts and Company
- 15 Goymann, W. *et al.* (2007) Distinguishing seasonal androgen responses from male-male androgen responsiveness—revisiting the Challenge Hypothesis. *Horm. Behav.* 51, 463–476

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Research Focus

Birds gone wild: same-sex parenting in albatross

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Same-sex behavior in animals fascinates scientists as well as laypeople, partly because of implications about sexual orientation in humans. After all, if animals engage in homosexuality, can it be dismissed as ‘unnatural’? A recent paper by Young and colleagues documents long-term female pairs in >30% of Laysan albatross on the Hawaiian island of Oahu. The unrelated females bred successfully, challenging ideas about cooperative breeding, alternative reproductive strategies and perhaps even the evolution of sexual orientation.

Same-sex behavior in wild birds

Sexual behavior directed toward the same sex has been noted in a variety of animals, including dolphins, sheep, penguins and bonobos [1]. Many of these instances have occurred in captivity, although in at least some cases members of the opposite sex were available as potential mates. By contrast, exclusively homosexual behavior has not been as well documented in wild animal populations, raising the question of its evolutionary relevance. A recent study by Young and colleagues [2] suggests that same-sex behavior in wild albatross colonies could have powerful and long-term effects on population dynamics. Of the 125 nests of Laysan albatross, *Phoebastria immutabilis*, examined by Young and colleagues on the Hawaiian island of Oahu, 31% were attended by a pair of females. This is more than twice the proportion of female pairs ever noted in any other bird species [2]. Two eggs were observed in half of those nests, but only one of them was ever incubated (albatross clutch size is one). Male–female pairs had higher reproductive success than the female pairs, but this was a result of lower hatching success in the same-sex nests rather than reduced fledging success. The males fathering the chicks in female–female nests were paired to other females in the colony, but were not necessarily the nearest neighbor. Partnered females were pair bonded, engaging in such intimate behaviors as mutual preening and mate guarding (Figure 1). The female pairs were remarkably stable, with nearly half

remaining together for the 4 years of the study; a female pair on the nearby island of Kauai has been together for 19 years. The population on Oahu has 59% females, probably as a result of female-biased recruitment to this relatively recently formed colony, and Young *et al.* suggest that the skewed sex ratio has driven the same-sex behavior, with a tendency toward social monogamy fostering its persistence.

Cooperation and alternative reproductive strategies

The behavior of the albatross has elements of both cooperative breeding, where individuals other than the parents help with offspring, and alternative reproductive strategies, where some members of one sex, usually males, exhibit a different path toward achieving mating success than the ‘standard’ strategy. The differences between the albatross and more traditional cooperative breeding or alternative reproduction, however, are instructive, and suggest that flexibility in social organization and mating systems might need to be viewed more broadly than is currently the case.

In conventional cooperative breeding, helpers can be constrained in their ability to breed on their own, so staying on their natal territory is a viable alternative [3]. Once the decision not to breed is made, helpers can increase their inclusive fitness by helping relatives, or they can gain valuable experience rearing offspring. Similarly, for some of the female albatross, the female-biased sex ratio might have meant that finding a male mate was impossible, but that the females were able to avoid complete loss of reproductive success by joining forces with another female. Whether one or both of the females mate, and which egg is incubated when two are laid, are open questions. Young and colleagues suggest that one egg is shunted aside at random during incubation. Although all social animals show elements of competition, the females do not appear to be competing overtly, making their situation at least superficially more similar to cooperative breeding than, for example, the communal nests of groove-billed anis, neotropical birds in which females throw each others’ eggs out of the nest depending on dominance status and the order in which they are laid [4].

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Figure 1. A female pair of Laysan albatross *Phoebastria immutabilis*. Photo by Alex Wegmann.

Although alternative reproductive strategies are known to occur in females, the phenomenon is usually associated with smaller or younger males that act as satellites or otherwise ‘sneak’ copulations that would ordinarily be obtained by territorial or dominant males [5]. Often the males pursuing such strategies have no other alternative, perhaps because of insufficient nutrition [5]. The albatross can be seen to be similarly ‘making the best of a bad job,’ because their reproductive success, although obviously higher than if they had simply not bred at all, was lower than that of mixed-sex pairs.

Along with these similarities, however, the albatross pairs pose some new challenges to conventional ideas about social and reproductive behavior. In some ways, they represent an intriguing hybrid of behaviors that have previously been classified as separate. Alternative reproductive strategies are thought to be relatively rare in females, perhaps because females are assumed to be able to produce offspring even if they are in poor condition. Yet low availability of males as social mates, such as in the albatross population, could be quite common, particularly in small, fragmented or recently founded populations. It is worth considering whether there are other conditions, such as sex-biased predation or differences in male and female life histories, which might favor females that follow a different path to reproductive success.

Remaining questions

The work of Young and colleagues prompts many exciting questions and avenues for further research. The most obvious question is how common such behavior might be in other species. Young and colleagues only discovered the high frequency of female pairs because they genetically sexed the birds; albatross, like most seabirds and many other animals, are sexually monomorphic, and researchers generally assume that pairs are heterosexual. Other colonially breeding species could harbor similar female pairs that have so far been overlooked by researchers.

Other issues arise from the unique demography of the population on Oahu. Will same-sex pairs stay together for the same amount of time as opposite-sex pairs, and does

fidelity depend on breeding success? How do females in same-sex pairs differ in morphology, age or condition from females in heterosexual pairs? And what does the future hold for the Oahu population? If more males become available, will the number of female pairs diminish?

Finally, how is selection acting on the females in same-sex pairs? Females that are more behaviorally flexible might be at an advantage, because participating in a same-sex pair increases fitness more than not breeding in a given season. If the high proportion of female pairs persists, perhaps the ability of the females to recognize their own eggs will improve, making competitive interactions between the females more likely.

Albatross and gay marriage?

The media were quick to exploit the same-sex behavior of the birds in the context of the growing movement for gay marriage, most recently approved by courts in California. One blogger filed the item under ‘perversion, science, sex’ [6]. Others claimed that the behavior of the birds contradicted the notion that homosexuality is ‘unnatural.’ Before we consider the merit of such claims, we might consider just what constitutes homosexuality in animals. The albatross were not observed to copulate, although this does not mean it did not occur, but their behaviors are clearly those of pair-bonded animals. Is it necessary to have sex to be considered homosexual? This question is clearly beyond the scope of the study. Until more work is done, we cannot tell whether the same-sex behavior is facultative among most females, or whether certain types of females are more likely to exhibit it regardless of the circumstances.

Whichever the case might be, Young and colleagues’ results suggest that such behavior can be adaptive in animals. Their success in connecting the dots between social dynamics, alternative mating strategies, cooperative breeding and fitness shows that researchers can gain fruitful insights into the evolution of same-sex behavior in any species, including our own. In other species such as guppies and *Drosophila*, same-sex behavior has been attributed to ‘prison effects’ [7], mistaken identity [8], aggression [1] or nonadaptive factors. In humans, a complex picture of homosexuality has emerged over the past few decades; neurobiologists have uncovered numerous differences between heterosexual and homosexual brains, and the genetics and evolutionary stability of homosexuality have been explored [9–11]. The study by Young and colleagues confirms the validity of studying same-sex behavior from an ecological and evolutionary perspective and, combined with recent theoretical and empirical work [10–12], suggests that what some dismiss as aberrant behavior can actually be a potent evolutionary force.

Acknowledgements

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References

- 1 Bagemihl, B. (2000) *Biological Exuberance: Animal Homosexuality and Natural Diversity*. Stonewall Inn Editions
- 2 Young, L.C. *et al.* (2008) Successful same-sex pairing in Laysan albatross. *Biol. Lett.* 4, 323–325

- 3 Koenig, W.D. and Dickinson, J.L., eds (2004) *Ecology and Evolution of Cooperative Breeding in Birds*, Cambridge University Press
- 4 Vehrencamp, S.L. (2000) Evolutionary routes to joint-female nesting in birds. *Behav. Ecol.* 11, 334–344
- 5 Brockmann, H.J. (2001) The evolution of alternative strategies and tactics. *Adv. Stud. Behav.* 30, 1–51
- 6 Irregular Times Diaries (2008) Unfit discussion (<http://irregulartimes.com/diaries/2008/05/albatross-lesbians>).
- 7 Field, K.L. and Waite, T.A. (2004) Absence of female conspecifics induces homosexual behaviour in male guppies. *Anim. Behav.* 68, 1381–1389
- 8 Macías-García, C. and Valero, A. (2001) Context-dependent sexual mimicry in the viviparous fish *Girardinichthys multiradiatus*. *Ethol. Ecol. Evol.* 13, 331–339
- 9 Savic, I. and Lindström, P. (2008) PET and MRI show differences in cerebral asymmetry and functional connectivity between homo- and heterosexual subjects. *Proc. Natl. Acad. Sci. U. S. A.* 105, 9403–9408
- 10 Gavrillets, S. and Rice, W.R. (2006) Genetic models of homosexuality: generating testable predictions. *Proc. Biol. Sci.* 273, 3031–3038
- 11 Camperio Ciani, A. *et al.* (2008) Sexually antagonistic selection in human male homosexuality. *PLoS ONE* 3, e2282
- 12 MacFarlane, G.R. *et al.* (2007) Same-sex sexual behavior in birds: expression is related to social mating system and state of development at hatching. *Behav. Ecol.* 18, 21–33

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Letters

Speciose versus species-rich

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The evolution of word use has contributed to the rich vocabulary of English in general and has made scientific English a particularly dynamic tool. However, some changes in word use have costs as well as benefits, and involve unintended consequences.

A widespread example of such a neologism is the description of species-rich taxa as ‘speciose.’ Although this word seems to be used mainly by evolutionary ecologists in the context of species diversity, it is derived not from ‘species’ but from the same Latin root as ‘specious,’ and shares with it a similar context of aesthetics and similar meaning of ‘beautiful, lovely’ [1].

The repurposing of ‘speciose’ has several benefits. By combining the new context (diversity) with the root meaning (beauty), the neologism inadvertently alludes to a moral value attached to species-rich taxa that is widely shared among evolutionary ecologists. Use of the neologism also conserves three consonants and an error-prone hyphenation in comparison to ‘species-rich.’ One cost to the user is the loss of the root meaning and the possibility of

referring to aesthetically pleasing organisms (rather than their taxonomic groups) specifically as ‘speciose.’ A second cost is the suffix shared with ‘verbose’ and the shared connotation that a simpler and more conventional phrase such as ‘species-rich’ might have done just as well.

‘Speciose’ and ‘species-rich’ first appeared in a searchable field of the Web of Knowledge database in 1957 [2,3]. Use of both phrases has greatly increased since (663 versus 2889 entries through 10 August 2008), including one case of ‘speciose’ in this journal [4]. A brief examination of the earliest and latest uses of ‘speciose’ suggested that all meant ‘species-rich’ and that the trend was not obviously slowed by Gill’s [5] plea to cease ‘the misuse of “speciose” in the evolutionary biological literature.’ From 1981 to 2007 (the longest period of continuous nonzero annual occurrence of ‘speciose’), the occurrence of ‘speciose’ was highly correlated with ‘species-rich’ ($r = 0.97$, $P < 0.001$), but the trend favored the neologism: the annual use of ‘speciose’ per use of ‘species-rich’ was significantly correlated with year ($r = 0.54$, $P = 0.003$; Figure 1), and was significantly

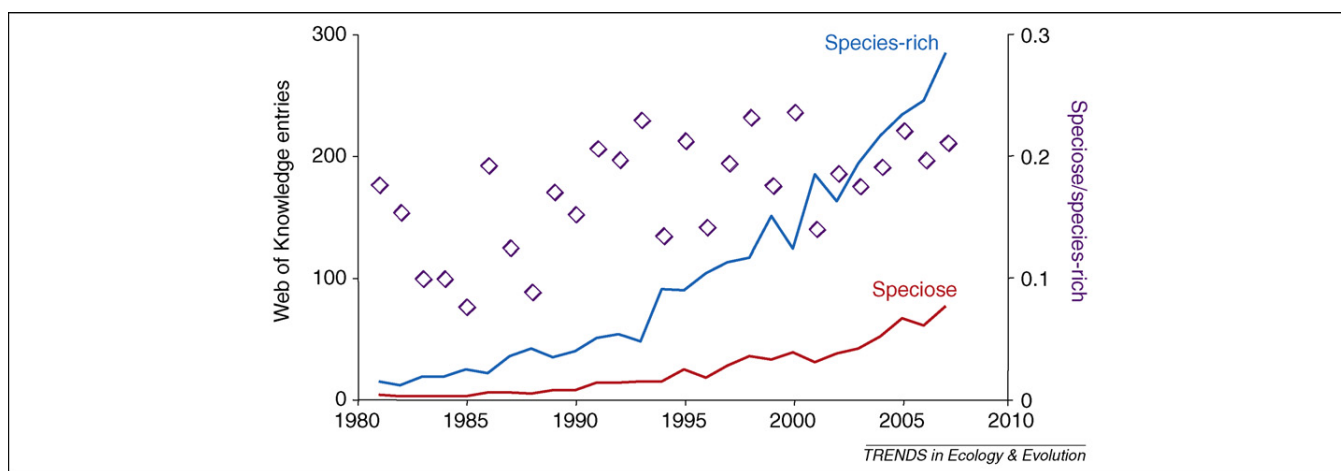


Figure 1. Lines show the trend in annual number of Web of Knowledge entries that used ‘speciose’ or ‘species-rich’ in a searchable field of the database from 1981 through 2007 (the longest continuous period of nonzero occurrence of ‘speciose’). A small number of entries (33) used both phrases. Open symbols show the significant increase in the relative frequency of occurrence of ‘speciose’.

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