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Swift declines predicted following mating system changes driven by an introduced predator

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Abstract

In Focus: Heinsohn, R., Olah, G., Webb, M., Peakall, R., & Stojanovic, D. (2019). Sex ratio bias and shared paternity reduce individual fitness and population viability in a critically endangered parrot. *Journal of Animal Ecology*, *88*, 502–510.

While the effects of variation in the sex ratio of offspring have been thoroughly explored over the last century, the sex ratio of adults has received far less attention. A paper by Heinsohn and colleagues in this issue shows that changes in the adult sex ratio can have striking effects on mating systems, reproductive success and population viability. These impacts are all the more dramatic because they occur in a critically endangered species, the swift parrot, *Lathamus discolor*, of Tasmania. This species suffers heavy predation from the introduced sugar glider, *Petaurus breviceps*, which kills nesting females and their clutches, resulting in strongly male-biased adult sex ratios. The authors combined demographic and genetic data to show that, at sites with heavier predation, the remaining females were more likely to mate with multiple males. This shift in the mating system also led to lower overall nesting success, with fewer chicks fledged per nest at sites with higher levels of mixed paternity. Population viability models based on these data predicted steep population declines, with models using the highest observed rates of mixed paternity showing the sharpest declines. These results demonstrate that changes in the adult sex ratio can have far-reaching impacts, including on the fitness of populations themselves.

KEYWORDS
adult sex ratio, invasive predator, mating system, parrot, polyandry, population fitness

There is a large body of both theoretical and empirical work on adaptive sex ratios—the notion that parents might skew the sex ratio among their offspring so as to maximize both their own and their offspring's fitness in a population with a given sex ratio (Hardy, 2002; Mayr, 1939; Sheldon, 1998; Trivers & Willard, 1973). Less attention has been paid to the potential effects of changes in the sex ratio of adults themselves (Donald, 2007; Mayr, 1939). This relative inattention can be explained in part because classical theory first proposed by Fisher (Fisher, 1930) predicts that changes in the adult sex ratio would be relatively transitory, because increased competition for mates or resources in the more common sex would lead to lower fitness for that sex and an eventual return to parity. In recent years, though, it has become increasingly apparent that adult sex ratios are often far from parity (Donald, 2007) and that changes in the adult sex ratio might have knock-on effects on mating systems, sex-specific fitness and population demographics (Holman & Kokko, 2013). Now, work by Robert Heinsohn and colleagues in this issue of the *Journal of Animal Ecology* provides a particularly striking example of such effects (Heinsohn, Olah, Webb, Peakall, & Stojanovic, 2019). They describe a system in which female-specific predation by an introduced predator has shifted the genetic mating system of a parrot from monogamy to polyandry, thereby reducing nestling survival with potentially devastating effects for an already declining population.

The parrot in question is the swift parrot, *Lathamus discolor*, a native of Australia. This species is unusual among parrots in that it is migratory, overwintering on mainland Australia and flying south to Tasmania in the austral summer to breed. It is also unusual in the extent to which it is nomadic in its breeding locations, which shift from year to year to follow the flowering of *Eucalyptus* species upon which it relies for nectar and the occasional lerp (Forshaw, 2017). It does resemble other parrots, however, in its dependence on the availability of secondary cavities for nesting. This dependency has led to population declines over the last few decades as old-growth forest is cleared in Tasmania (Forshaw, 2017). In recent years, this decline has been greatly exacerbated by a growth in the population of sugar gliders, *Petaurus breviceps*. These small possums were introduced to Tasmania from mainland Australia around 1835 and since the 1940s have spread rapidly across most of the main island of Tasmania, including much of the remaining old-growth forest favoured by the swift parrot (Allen, Webb, Alves, Heinsohn, & Stojanovic, 2018; Campbell et al., 2018). They have proven to be devastating predators of the swift parrot, invading active nests at night and killing both the females and their nestlings while they sleep (Stojanovic, Webb, Alderman, Porfirio, & Heinsohn, 2014). Demographic studies coupled with population viability analysis from a team lead by Heinsohn and colleagues Dejan Stojanovich and Matthew Webb have already predicted rapid population declines due to this novel predator (Figure 1, see also Heinsohn et al., 2015). In the current paper, they have expanded on this work by considering the more insidious effects that this sex-specific predation has on adult sex ratios, the mating system of the species, and ultimately, population viability.

The authors collected data on the nesting success over 6 years from seven sites across Tasmania. Importantly, these sites are located both on the main island of Tasmania, where sugar gliders are well-established, and on two offshore islands where the predator is not yet present. They then paired these data with genetic data from microsatellites to genotype offspring and determine the level of extra-pair paternity in 85 nests. They found, not unexpectedly, that nest predation rates were far lower at sites where

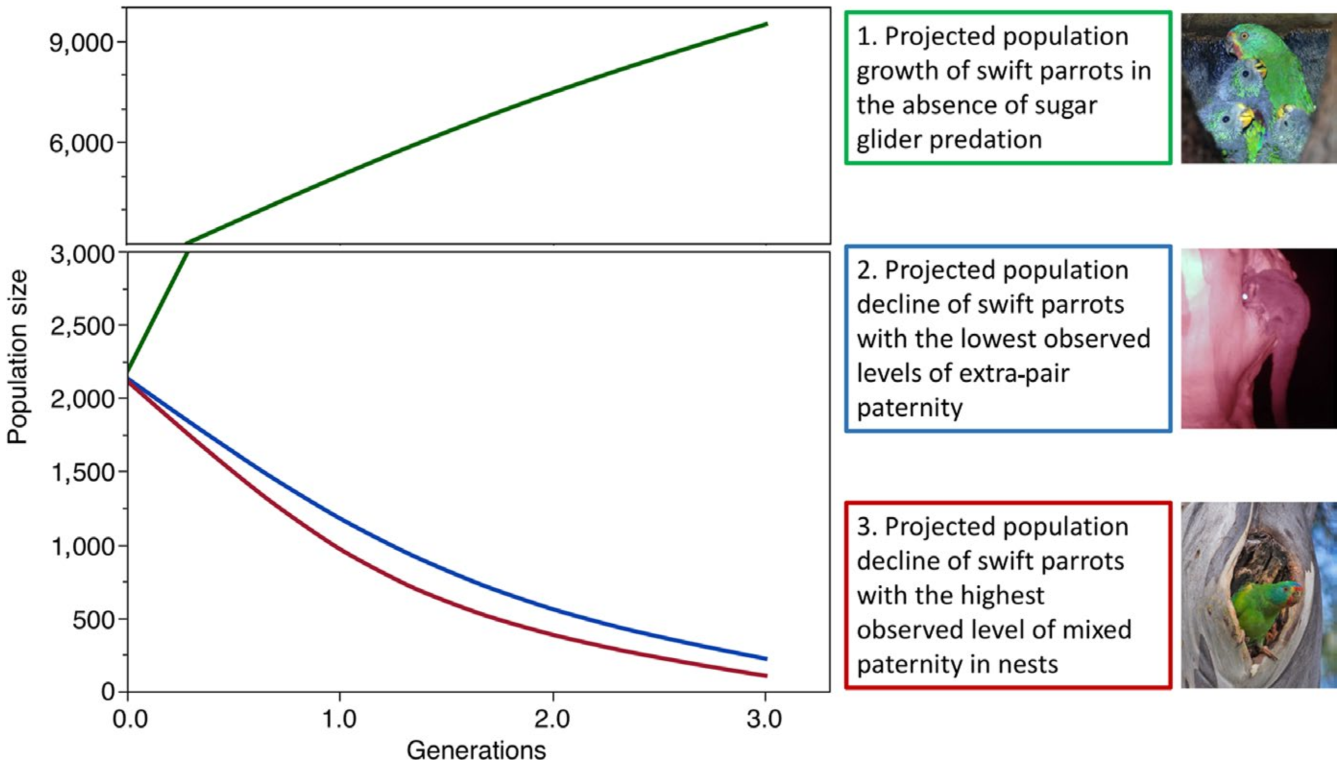

FIGURE 1 Swift parrots are a nomadic species that breeds in the old-growth forests of Tasmania. Their cavity-nesting habits have rendered them vulnerable to predation by introduced sugar gliders. Predation on nesting females reaches in excess of 50% of nests at some sites and results in a strongly biased male adult sex ratio. A study by Heinsohn et al. (2019) in this issue has found that sites with higher predation also have much higher rates of mixed paternity in nests and fledge fewer chicks per nest. These changes in female mating from predominantly monandrous to predominantly polyandrous are predicted to also have strong effects on population viability in this already endangered parrot. In green is the projected population growth of swift parrots in the absence of sugar glider predation; under these conditions, the global population is projected to grow by >300% over three generations (16 years). In blue is the projected population decline in the presence of sugar glider predation with the lowest rates of polyandry and highest fledging success, a decline of 89% over three generations. In red is the predicted outcome with the highest observed rates of polyandry and lowest fledging success; these conditions are predicted to lead to a shocking decline of 95%, to a global population of only 150 adults. These results provide a novel and striking example of how changes in the adult sex ratio can have indirect effects on multiple aspects of a population's biology and, ultimately, its fitness. Photographs on the right depict (a) a female swift parrot with three chicks, (b) a predatory sugar glider entering a swift parrot nest at night and (c) a male swift parrot at the entrance hole of a nest; all photographs by Dejan Stojanovic

sugar gliders were present (14%–54% of nest predated) than at sites where sugar gliders were not established (0–8% of nest predated). More surprising though, were the effects that this predation had on the mating system. In sites without the sugar glider, extra-pair paternity was about 30%, perhaps higher than might be expected in a parrot with social monogamy and extensive male care of both females and nestlings, but nothing to prompt raised eyebrows. Mixed paternity rate climbed dramatically, though, as sugar glider predation became more common, to a high of 95% of nests showing mixed paternity at sites with the highest predation rates. The authors attribute this shift in the genetic mating system, from predominantly monandry to predominantly polyandry, to the strong male bias in the adult sex ratio driven by the sex-specific predation on females. This male bias in turn leads to stronger competition among males for mating opportunities with the remaining females, and an increase in the percentage of females that mate with multiple males. Notably, this shift in the genetic system was not accompanied by a shift in the social mating system, which remained monogamous with extensive care by a single male. Nonetheless, multiple mating was costly to females, as successful nests at sites with higher rates of mixed paternity fledged on average 1 fewer chick than successful nests at sites with lower mixed paternity. This lowered success was not due to a difference in the clutch size of nests with single versus multiple fathers. Instead, this differential survival seemed to arise again from the increased competition among males, which was hypothesized to interfere with the social father's efforts to provision the mother and her chicks during the nestling stage.

The authors went on to incorporate these data on predator-induced declines in fledging success into a new series of models in order to predict effects on swift parrot population viability. The results were striking. Their previous population viability models incorporating sugar glider predation predicted drastic declines in population size, with the average prediction across models of an 87% decline over three generations. As illustrated in Figure 1, a baseline model that did not include this predation actually predicted an increase in population size of 340% over the same time span (Heinsohn et al., 2015). The new models incorporated their data on fledging success rates at different levels of mixed paternity. These models predicted that, under the lowest level of mixed paternity observed, the population would decline by 89% over three generations to about 240 individuals, roughly the same as the average of previous models, while at the highest level of mixed paternity (with the lowest fledging success), the population would decline by 95% over three generations to about 125 individuals (Heinsohn et al., 2019). These models clearly demonstrate that sugar glider predation is having negative effects on population fitness, both directly through adult and offspring mortality, and indirectly through decreased fledging success driven by changes in the adult sex ratio (Figure 1). Happily, conservationists have been quick to respond and efforts are now underway to control sugar glider populations and to provide safer nesting options for swift parrots to reduce sugar glider predation (Stojanovic et al., 2019).

There are certainly some limitations to this work, as might be expected for a field study on a rare and elusive species. Perhaps chief among them is that the causal links between mating system changes and decreased fledging success remain to be worked out. The authors suggest that this effect is due to either increased harassment of females or decreased attention from the social male, but both are yet to be quantified. Furthermore, although this effect on fledging success is seen at the site level, when examined within sites, nests with mixed paternity showed no higher fledging success than nests completely fathered by the social male. Although perplexing, these results do argue against one alternative hypothesis, that polyandrous females are poorer mothers than monandrous ones. Another possibility, as yet unexplored, is that decreased relatedness within nests increases competition among offspring and reduces their overall survivorship. These caveats notwithstanding, the work is striking for the way it combines field-generated demographic data, genetic data and population modelling to demonstrate effects of an altered adult sex ratio that may have been predicted before on theoretical grounds, but have rarely been demonstrated (but see Carrete, Donázar, Margalida, & Bertran, 2006). The fact that these effects occur in a species where they have a life-or-death impact makes them all the more noteworthy. More generally, these results suggest that increased attention to the potentially subtle and indirect effects of altered adult sex ratios could uncover further surprises for ecologists and conservation biologists alike.

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REFERENCES

Allen, M., Webb, M. H., Alves, F., Heinsohn, R., & Stojanovic, D. (2018). Occupancy patterns of the introduced, predatory sugar glider in Tasmanian forests. *Austral Ecology*, *43*, 470–475. https://doi.org/10.1111/aec.12583

Campbell, C. D., Sarre, S. D., Stojanovic, D., Gruber, B., Medlock, K., Harris, S., … Holleley, C. E. (2018). When is a native species invasive? Incursion of a novel predatory marsupial detected using molecular and historical data *Diversity and Distributions*, *24*, 831–840. https://doi.org/10.1111/ddi.12717

Carrete, M., Donázar, J. A., Margalida, A., & Bertran, J. (2006). Linking ecology, behaviour and conservation: does habitat saturation change the mating system of bearded vultures? *Biology Letters*, *2*, 624–627. https://doi.org/10.1098/rsbl.2006.0498

Donald, P. F. (2007). Adult sex ratios in wild bird populations. *Ibis*, *149*, 671–692. https://doi.org/10.1111/j.1474-919X.2007.00724.x

Fisher, R. A. (1930). *The genetical theory of natural selection*. Oxford, UK: Clarendon Press. https://doi.org/10.5962/bhl.title.27468

Forshaw, J. M. (2017). *Vanished and vanishing parrots: Profiling extinct and endangered species*. Ithaca, NY: Comstock Publishing Associate. https://doi.org/10.1071/9780643106499

Hardy, I. C. W. (Ed.) (2002). *Sex ratios: Concepts and research methods*. Cambridge, UK: Cambridge University Press.

Heinsohn, R., Olah, G., Webb, M., Peakall, R., & Stojanovic, D. (2019). Sex ratio bias and shared paternity reduce individual fitness and population viability in a critically endangered parrot. *Journal of Animal Ecology*, *88*, 502–510.

Heinsohn, R., Webb, M., Lacy, R., Terauds, A., Alderman, R., & Stojanovic, D. (2015). A severe predator-induced population decline predicted for endangered, migratory swift parrots (Lathamus discolor). *Biological Conservation*, *186*, 75–82. https://doi.org/10.1016/j.biocon.2015.03.006

Holman, L., & Kokko, H. (2013). The consequences of polyandry for population viability, extinction risk and conservation. *Philosophical Transactions of the Royal Society B-Biological Sciences*, *368*, 12.

Mayr, E. (1939). The sex ratio in wild birds. *The American Naturalist*, *73*, 156–179. https://doi.org/10.1086/280824

Sheldon, B. C. (1998). Recent studies of avian sex ratios. *Heredity*, *80*, 397–402. https://doi.org/10.1046/j.1365-2540.1998.00374.x

Stojanovic, D., Cook, H. C. L., Sato, C., Alves, F., Harris, G., McKernan, A., ... Heinsohn, R. (2019). Pre-emptive action as a measure for conserving nomadic species. *Journal of Wildlife Management*, *83*, 64–71. https://doi.org/10.1002/jwmg.21575

Stojanovic, D., Webb, M. H., Alderman, R., Porfirio, L. L., & Heinsohn, R. (2014). Discovery of a novel predator reveals extreme but highly variable mortality for an endangered migratory bird. *Diversity and Distributions*, *20*, 1200–1207. https://doi.org/10.1111/ddi.12214

Trivers, R. L., & Willard, D. E. (1973). Natural-selection of parental ability to vary sex-ratio of offspring. *Science*, *179*, 90–92. https://doi.org/10.1126/science.179.4068.90

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