

Short communication

Sex differences in incubation behaviour but not mortality risk in a threatened shorebird

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Sex-related variation in survival is common in birds and, as it influences effective population size and population growth, is important for conservation and species management. Here we assessed incubation behaviour and sex-related survival in a threatened sexually monomorphic shorebird, the St Helena Plover *Charadrius sanctaehelena*. Males incubated at night, the period of highest activity of cats, which are likely to be predators of breeding birds. In spite of behavioural differences between the sexes, adult survival was not significantly different between males and females, suggesting that sex-biased behaviour need not lead to sex-related survival, and thus behavioural differences may not impact upon the adult sex ratio.

Keywords: conservation, demography, sex-related survival, St Helena Plover, wader, Wirebird (synonym).

Adult sex ratio (ASR) is one of the key demographic traits influencing population dynamics (Lee *et al.* 2011). ASR is usually skewed toward males in birds and is primarily attributable to higher adult female mortality (Donald 2007). Understanding patterns of, and reasons underlying, ASR and sex-related demography can inform species conservation (e.g. Clout *et al.* 2002). Differential survival can influence the effective population size and therefore the population growth rate. Gruebler *et al.* (2008) found that a population of Eurasian Whinchats *Saxicola rubetra* was declining 1.7 times faster than

anticipated because adult mortality was differentially affecting incubating females. Furthermore, a skewed ASR may affect a population's ability to recover, in particular if males are over-represented (Bessa-Gomes *et al.* 2004). Donald (2007) found that threatened birds consistently exhibited more male-biased ASRs than non-threatened ones.

Here we investigate parental behaviour in an endangered shorebird, the St Helena Plover *Charadrius sanctaehelena* (BirdLife International 2009, McCulloch 2009), endemic to the Atlantic island of St Helena, to assess whether behavioural differences in incubation are associated with sex-related adult survival. Previously we showed that clutch survival is low (average clutch survival = 21.5%) and that the majority (80%) of nest predation occurs at night. The most common predator recorded was the domestic cat *Felis catus*, followed by rats *Rattus norvegicus* or *Rattus rattus*, and Common Myna *Acridotheres tristis* (Burns *et al.* 2013a). Although direct evidence is scarce for other life stages, it is likely the same species prey upon chicks and that cats are the main predator of adults (McCulloch 2009). As cats are mostly active at night, we conjectured that this may lead to reduced survival of the sex that incubates at night. If, like many other threatened bird species, survival is sex-related in the St Helena Plover, increasing predation pressure may have a compound effect on the species' persistence. Investigating sex-related differences in behaviour and mortality, however, is challenging in sexually monomorphic species such as the St Helena Plover. We therefore used molecular markers (Ellegren 1996, Griffiths *et al.* 1998, Dos Remedios *et al.* 2010) to sex adult and young St Helena Plovers.

The aim of this study was to assess whether incubation patterns or survival are sex-related in the St Helena Plover. If there is a bias towards one sex undertaking the majority of nocturnal incubation, we predict that its survival may be suppressed.

METHODS

On St Helena (15°58'S, 5°43'W) data were collected at the main breeding sites: Deadwood Plain, Broad Bottom, Man and Horse, Upper Prosperous Bay and Prosperous Bay Plain (locations shown in McCulloch 2009). The first three sites are pasture areas and the others semi-desert. Fieldwork was carried out during 2007–2010 in three field seasons, the first two November to February, and the third January to February. Birds were ringed during the first two field seasons (Burns *et al.* 2010). Trapping was done during daylight. Chicks were caught by hand, measured and given a BTO metal ring at hatching and individually colour-ringed at 2 weeks. During the second field season blood samples, c.25 µL, were taken for molecular sexing. Molecular sexing using faecal

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samples from field season 1 was unsuccessful, as the volume of DNA extracted was insufficient for analysis. Data from 34 juveniles (30 genetically sexed as chicks and four by mating behaviour when adult) and 64 adults were used in our analysis. Of the adults, 39 were sexed using blood samples and 35 from mating behaviour or having a known sex mate. Sex of all individuals that were sexed using both methods agreed ($n = 10$). DNA was extracted using the ammonium acetate method (Richardson *et al.* 2001). CHD-Z and CHD-W genes were amplified via PCR using the P2/P8 primers (Griffiths *et al.* 1998). For additional certainty in sex assignment, the Z-002B/Z-002D primers (D.A. Dawson unpubl. data) were used. IR dye-labelled tailed primers separated the product of Z-002B/Z-002D and P2/P8 primers into one (ZZ) or two bands (ZW), indicating male or female, respectively.

Incubation behaviour was scored using footage from small (2.5-cm diameter), motion-sensitive cameras with infrared light arrays (male, female or neither on the nest) (Bolton *et al.* 2007). Activities of less than 10 s duration were not scored. Seven 24-h periods were recorded from five nests where the sexes could be identified. The recordings are from nests of different ages, but all had a complete clutch of two eggs (modal clutch size) prior to camera installation. A mixed model with binomial errors was used to investigate the balance of female to male incubation throughout the day. A categorical factor with two levels that differentiated between night and day was used as an explanatory variable, and nest identity and 24-h period were used as random factors. The binomial denominator was total incubation duration (minutes) and the two-vector response variable, signifying the total incubation duration for females and males, estimated separately for day and night. The analysis was done using PROGRAMME R (R Core Development & Team 2004).

Apparent survival (Φ) and resighting probability (p) for adults and juveniles were estimated using MARK (White & Burnham 1999). The complement of apparent survival is mortality plus permanent emigration. For St Helena Plovers the latter will be small as they do not disperse from the island and resighting efforts covered all known sites. Resighting was carried out on five occasions: November 2008, February 2009, August 2009, October 2009 and January–February 2010. The final resighting period was a year after ringing stopped, at which time all birds ringed as chicks would have reached adulthood. Only juveniles known to have fledged were included, to differentiate between chick and juvenile survival, the latter taken as survival from fledging to 1 year. Due to the short duration of the study, temporal variation in survival was not investigated. Analysis included known-sex birds only and all birds aged 1 or older were classed as adults, juveniles changing category to become adults upon reaching

1 year old. Adults and juveniles were treated separately in the analysis, as survival is generally substantially lower for young animals prior to reaching sexual maturity. The general model was $\Phi(\text{sex}) p(\text{sex})$, for adults and juveniles. Goodness-of-fit testing used median \hat{c} and models were adjusted accordingly. First, we compared a series of models with different recapture terms, testing for temporal variation in recapture or sex-related variation in recapture for both adults and juveniles. The most parsimonious model was selected as that with the lowest Akaike information criterion (AIC). The most parsimonious recapture term was then used in a second series of models investigating sex-related survival, again using AIC to select the most parsimonious model.

RESULTS

Nests were incubated 77% of the time and an intercept-only version of the mixed model showed that male and female incubation duration did not differ over the 24-h period ($t_7 = -0.309$, $P = 0.766$; 0.48 of total incubation by females; Fig. 1). The balance of incubation between males and females was significantly different between the daylight period (sunrise 05:56 h to sunset 18:55 h) and at night (mixed model, $t_6 = 3.367$, $P = 0.015$; Fig. 1). During daylight, females incubated more than males (65% of total incubation), whereas they incubated far less during the night (24% of total incubation).

There was no support for sex-related survival or resighting for adults or juveniles (Table 1, monthly adult

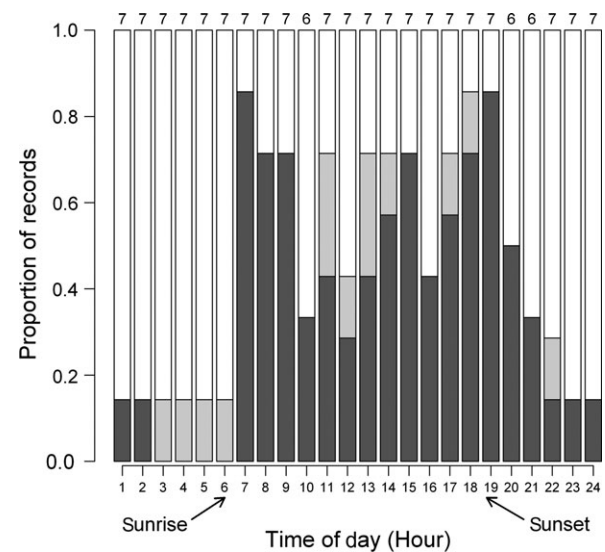


Figure 1. Incubation on each hour by female (dark grey) and male (white) St Helena Plovers. Light grey indicates that neither parent is on the nest; n is given above each bar.

Table 1. Survival analysis of adult (A) and juvenile (J) St Helena Plover using MARK.

Model specification		$n = 64_A (26_M38_F), 34_J (17_M17_F)$			
Survival	Resighting	Δ QAIC	K	Deviance	Weight
Φ_A, Φ_J	p_A, p_J^a	0	4	343.870	0.413
Φ_A (sex), Φ_J	p_A, p_J	1.337	5	343.145	0.212
Φ_A, Φ_J (sex)	p_A, p_J	1.572	5	343.380	0.188
Φ_A (sex), Φ_J (sex)	p_A, p_J	2.903	6	342.638	0.097
Φ_A (sex), Φ_J (sex)	p_A, p_J (sex)	4.773	7	342.422	0.038
Φ_A (sex), Φ_J (sex)	p_A (sex), p_J	5.232	7	342.880	0.030
Φ_A (sex), Φ_J (sex) ^b	p_A (sex), p_J (sex)	7.080	8	342.629	0.012
Φ_A (sex), Φ_J (sex)	p (time)	7.347	9	340.784	0.010

K, number of parameters; Φ_A , adult survival; Φ_J , juvenile survival; p_A , adult resighting probability; p_J , juvenile resighting probability. M and F are used to denote males and females, respectively. ^a $p_A = 0.766$ (0.701–0.820), $p_J = 0.529$ (0.312–0.699). ^bStarting model on which goodness-of-fit testing was done, $\hat{c} = 1.006$.

survival (Φ_A) = 0.977 (95% confidence limit (CL): 0.966–0.985), annual $\Phi_A = 0.758$ (0.656–0.833), monthly juvenile survival (Φ_J) = 0.940 (0.895–0.966), fledging to 1-year $\Phi_J = 0.536$ (0.328–0.708). Birds of known sex make up only a subset of birds ringed (around 60% of ringed adults are of known sex). Equivalent values for the full dataset, including unsexed birds, give annual $\Phi_A = 0.829$ (0.748–0.887) and fledging to 1-year $\Phi_J = 0.471$ (0.325–0.606) (Burns *et al.* 2013b). Burnham and Anderson (2002) suggest that models within two AIC units of the minimum should be considered for model averaging. The difference between the top and second placed model, which includes sex-related adult survival, is 1.34 AIC units. Nevertheless, the 95% CL for female and male survival in the latter model are largely overlapping, lending little support for sex-related survival (monthly ♀ $\Phi_A = 0.981$ (0.965–0.989), monthly ♂ $\Phi_A = 0.973$ (0.953–0.984)).

DISCUSSION

The survival of male St Helena Plovers could be compromised if they incubate largely at night, like males of several other *Charadrius* species (Kosztolányi & Székely 2002, St Clair *et al.* 2010), as this is the active period of most predators of breeding plovers on St Helena. Amat and Masero (2004) found male Kentish Plovers *Charadrius alexandrinus*, which show similar partitioning of incubation, were more likely to be predated at the nest than females. They attributed this to lower visibility at night, and therefore poorer escape responses. Additionally, it has been suggested that the female-biased sex ratio of the Stewart Island population of the New Zealand Dotterel *Charadrius obscurus* developed due to lower male survival during night time incubation (Dowling *et al.* 1999). Whether males or females are at greater risk will depend, however, on the local predator

community. For instance, Two-banded Plovers *Charadrius falklandicus* show a similar incubation pattern but females may be at greater risk, as all nest predations were filmed during daylight (St Clair *et al.* 2010). Despite several comprehensive studies of shorebird species, few have observed sex-related adult survival (Larson *et al.* 2000, Sandercock *et al.* 2005, Stenzel *et al.* 2011), in contrast to other bird groups, in which females often have lower survival (e.g. Promislow *et al.* 1992, Gruebler *et al.* 2008). Sex-related adult survival may be rare amongst shorebirds partly because incubation is generally shared, compared with female-only incubation in other groups. Indeed, the male-biased ASR of many threatened bird species is thought to be largely attributed to the predation of incubating females (Donald 2007).

There are several possible reasons why we did not detect sex-related adult survival despite the fact that male Plovers incubated during the active period of the majority of predator species. First, if anti-predator behaviours are efficient even during the active period of predator species, predation may have little influence on the survival of either sex. Early flushing from the nest is the Plover's main response to potential predators of adults. Secondly, as survival is influenced by many aspects of the environment it could be difficult to detect the influence of predation. Indeed, if the effects of other environmental variables on adult survival are also sex-related, they may balance out any influence of nocturnal predation on male survival. Finally, this is a rare and endangered species, and thus sample sizes are moderate and may lack sufficient power to detect small effect sizes.

Although predation from introduced species may be a conservation issue for St Helena Plovers, it appears unlikely that sex-related adult survival is exacerbating this. The absence of sex-related survival suggests that St

Helena Plovers may have retained effective anti-predator behaviour from their ancestral forms that may have encountered nocturnal predators, despite the absence of native nocturnal predators on St Helena. One of the extinct rails endemic to St Helena may, however, have been an occasional egg-eater (Olson 1975). Finally, knowledge of sex-related demography also informs our understanding of the species' population dynamics and will advise conservation management.

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