



## Parasite Treatment Affects Maternal Investment in Sons

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24. The divergence between ITQ and non-ITQ fisheries is even more pronounced for less conservative definitions of collapse; i.e. 1 to 6% of historical maximum catch (Fig. 1B).
25. The LMEs with at least one fishery managed using an ITQ by 2003 are the California Current, Gulf of Alaska, Humboldt Current, Iceland Shelf, New Zealand Shelf, Scotian Shelf, Southeast Australian Shelf, Southeast U.S. Continental Shelf, Southwest Australian Shelf, and West-Central Australian Shelf.
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27. We thank the Paul G. Allen Family Foundation for generous financial support; the Sea Around Us Project for

making the catch data publicly available; C. Wong and T. Kidman for helping to compile the database; B. Hansen for helpful comments; and J. Prince, K. Bonzon, and J. Toth for assisting with verifying the catch-share database.

#### Supporting Online Material

www.sciencemag.org/cgi/content/full/321/5896/1678/DC1  
Materials and Methods  
SOM Text  
Figs. S1 and S2  
Tables S1 to S5  
References

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## Parasite Treatment Affects Maternal Investment in Sons

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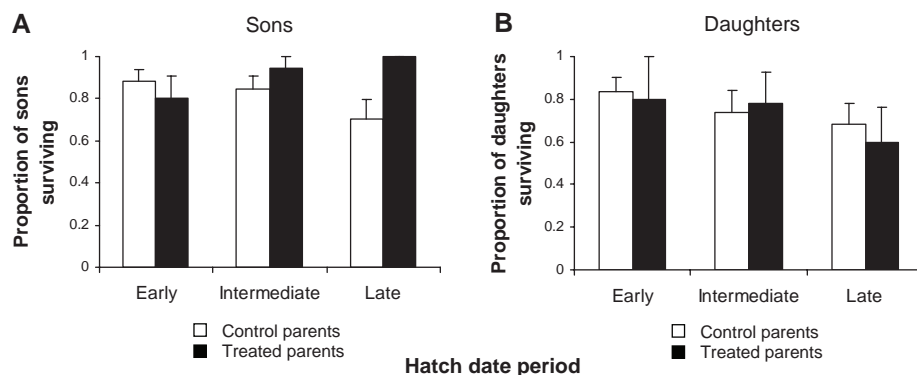
Parasitism can be a major constraint on host condition and an important selective force. Theoretical and empirical evidence shows that maternal condition affects relative investment in sons and daughters; however, the effect of parasitism on sex ratio in vertebrates is seldom considered. We demonstrate experimentally that parasitism constrains the ability of mothers to rear sons in a long-lived seabird, the European shag *Phalacrocorax aristotelis*. The effect contributes to the decline in offspring survival as the breeding season progresses and hence has important population-level consequences for this, and potentially other, seasonal breeders.

One key ecological factor influencing the condition of parents, and therefore the potential fitness of dependent offspring, is parasitism (1). In sexually dimorphic species, offspring of the larger sex often require higher nutritional investment and are more vulnerable to changes in parental condition (2). Moreover, sex allocation theory predicts that parents in good condition should bias investment toward offspring of the sex that stands to gain more from extra resources provided at critical developmental stages (3). We provide experimental evidence that parasites can constrain the ability of mothers, in particular, to rear offspring of the more expensive sex. This contributes to differential mortality of sons and daughters as the breeding season progresses and could explain the seasonal decline in offspring survival that is commonly observed in this and many other seasonal breeders.

Populations of the European shag *Phalacrocorax aristotelis* frequently suffer from severe infections of gastro-intestinal parasites, in particular anisakid nematodes [*Contracaecum rudolphi* and *Anisakis simplex* (4)]. Although their effects are usually sublethal, these parasites compete with the host for nutrients and trigger costly immune responses (5) that may impair host breed-

ing success. Shag chicks must be provisioned in the nest for ~50 days by both parents. Male-biased broods require more food than female-biased broods, and male nestlings grow faster, attain higher peak masses at fledging, and are about 20% larger than females as adults (4).

We experimentally manipulated parasitism levels in breeding adults just before chick hatching by treating both male and female parents with a broad-spectrum antiparasite drug (ivermectin), which removes gut parasites and prevents reinfection over a period of ~6 weeks and hence for most of the chick-rearing period. Throughout the laying period, nests were randomly allocated to either a treatment group, in which both parents were treated with ivermectin ( $n = 34$  nests), or a control (untreated) group in which parents were exposed to natural levels of parasitism ( $n = 83$  nests). Treated and control nests were matched for laying date, ensuring an equal spread of laying dates in each group spanning the natural range (~6 weeks). The survival of sons was higher when their parents had been treated (Fig. 1A) [generalized linear mixed model

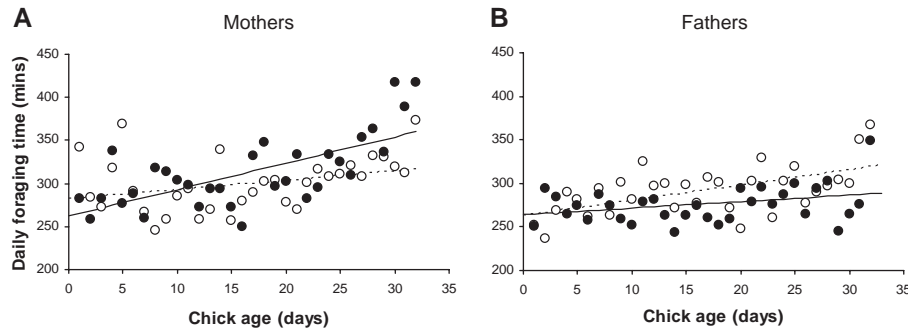


**Fig. 1.** Differential effect of ivermectin treatment on survival of sons (A) and daughters (B), and interaction with hatch date. Black bars represent chicks from treated parents, and white bars chicks from control parents. Hatch dates are grouped into early, intermediate and late periods, based on thirds of the distribution and corresponding roughly to 2-weekly intervals. The decline in the survival of sons is not apparent when their parents have been treated. Parasite treatment did not appear to affect the success of rearing daughters. Overall, parasitism in parents accounted for ~37% of the natural seasonal decline in chick survival. Data are means  $\pm$  SEM. Effect sizes and statistics from logistic regression are given in the text.

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**Fig. 2.** Effect of the dosing procedure on average time spent foraging each day by mothers (**A**) and fathers (**B**) as chicks get older. Treated parents in both cases are represented by closed circles with a solid line showing the effect, and untreated (control) parents are indicated by open circles and a dashed line. The  $x$  axes show the age of the oldest chick in nests where the foraging effort of the parents was measured, and data points represent the mean daily time spent foraging by parents at each of these ages (day 0 is the day the first chick hatched). Mothers increased their foraging effort when treated with ivermectin, but fathers appeared to reduce theirs. Linear effects are best fits from the mixed-effects models, and statistics and sample sizes are given in the text.

(GLMM): treatment  $\times$  chick sex interaction,  $\chi^2 = 7.92$ ,  $P = 0.005$ ; treated:  $90.7 \pm 4\%$  (SEM) surviving; controls:  $81 \pm 4\%$  surviving]. This was not the case for daughters (Fig. 1B) (treated:  $71 \pm 9\%$  surviving; controls:  $76 \pm 5\%$  surviving).

Parasitism can have population-level consequences. Like many birds, European shags that breed later in the season show reduced breeding success. In our study population, breeding 3 weeks after the population mean resulted in a 21% reduction in breeding success (GLMM of chick survival, date effect:  $b = -0.123 \pm 0.032$ ,  $\chi^2 = 15.34$ ,  $P < 0.001$ ), mainly due to poorer survival of male chicks (decline in male survival:  $b = -0.162 \pm 0.038$ ; female survival:  $b = -0.078 \pm 0.038$ ;  $\chi^2 = 5.70$ ,  $P = 0.025$ ). However, following ivermectin treatment, the decline in offspring survival was significantly reduced in the group with treated parents compared with the control group (GLMM: treatment  $\times$  hatch date interaction,  $\chi^2 = 4.25$ ,  $P = 0.039$ ; decline in controls:  $b = -0.139 \pm 0.065$ , treated:  $b = -0.088 \pm 0.031$ ). This effect was driven by the increased survival of male chicks from treated pairs (GLMM: treatment  $\times$  hatch date  $\times$  chick sex interaction,  $\chi^2 = 8.85$ ,  $P = 0.003$ ), such that declines were no longer apparent for sons (Fig. 1A).

To examine possible reasons why sons were reared more successfully by ivermectin-treated parents, we used activity loggers to compare the foraging performance of treated and untreated males and females. As chicks became older, parents increased their foraging effort, but the patterns were different for treated mothers and treated fathers (Fig. 2) [linear mixed effects model (LMM): treatment  $\times$  parental sex  $\times$  chick age interaction,  $n = 14$  mothers,  $n = 16$  fathers;  $\chi^2 = 9.65$ ,  $P = 0.002$ ]. Treated mothers spent more time foraging as their chicks became older relative to control mothers (Fig. 2A) (LMM for mothers only: treatment  $\times$  chick age interaction,  $\chi^2 = 6.27$ ,  $P = 0.013$ ). Treated fathers, by contrast, tended to reduce their effort through the

chick-rearing period relative to control fathers (Fig. 2B) (LMM for fathers only: treatment  $\times$  chick age interaction,  $\chi^2 = 2.80$ ,  $P = 0.095$ ). Treated parents did not maintain body mass over the chick-rearing period any better than control parents (average mass lost by  $n = 10$  treated birds, mothers and fathers combined, was  $39.0 \pm 37.9$  g, and  $23.3 \pm 32.3$  g for  $n = 15$  control birds;  $t = 0.311$ ,  $P = 0.758$ , no significant sex differences) and presumably were not allocating additional resources to themselves. The treated mothers, it seems, passed the nutritional benefits on to their sons. Treated fathers may have reduced their investment in the brood as a whole (and so spent less time foraging) in response to a perceived increase by their partners. The net effect, nevertheless, was an increase in the survival of sons from treated nests, suggesting that sons benefited from increased maternal investment regardless of any reduction in effort by their fathers.

Given that mothers suffering from infection struggle to rear sons, should they not then prioritize investment in daughters? If so, we would expect the daughters of control parents to survive better than sons. This pattern was observed in the first year of the study, but not the second year. Environmental conditions were poor in 2005, and productivity in the colony was low. As expected, survival of daughters was significantly higher ( $83 \pm 9\%$ ) than that of sons ( $58 \pm 11\%$ ) for untreated pairs in this year ( $n = 27$  nests,  $\chi^2 = 10.97$ ,  $P = 0.003$ ). In contrast, conditions were much more favorable in 2006 (and overall productivity much higher), and untreated parents were more successful at rearing sons (survival of daughters =  $74 \pm 6\%$ , survival of sons =  $87 \pm 4\%$ ,  $n = 56$  nests,  $\chi^2 = 6.58$ ,  $P = 0.012$ ). When resources are limited, it appears that mothers preferentially invest in daughters, and only when conditions improve do they shift the balance of resources over to sons. The effect that parasitism has on parents' ability to rear sons may depend, therefore, on environmental quality, most obviously the availability of food.

We have shown that the costs of parasitism to mothers can have a differential effect on the survival of male and female chicks, large enough to induce a marked decline in chick production in the population during the breeding season. Parasite prevalence tends to increase as the season progresses (fig. S1), and hence late breeders may suffer higher burdens. Late breeders may be also more susceptible to infection or its associated costs (6), because they tend to be in poorer physiological condition, less experienced, and less capable of mounting effective immune responses (7). Previous studies have shown that maternal condition can be a key factor in determining primary offspring sex ratio in birds (8), and parasitism has many well-documented effects on primary sex ratio in invertebrates (9). Our study illustrates that parasitism may be a key factor in limiting secondary sex ratio, but the effects of parasitism and its interaction with maternal condition on primary sex ratio in wild bird populations remains untested. Untangling these potentially interacting effects remains a challenge, but it is clear that parasites can have a substantial impact on the relative success of rearing male and female offspring.

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SOM Text

Fig. S1

References

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