THESIS

ADJUSTMENTS TO PARENTAL CARE BY THE EUROPEAN STARLING (*STURNUS VULGARIS*): THE EFFECT OF FEMALE CONDITION

Submitted by

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In partial fulfillment of the requirements for the
Thesis in Zoology
Weber State University
Ogden, Utah
December 2003

WEBER STATE UNIVERSITY

WE HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER OUR SUPERVISION BY HEATHER HILL ENTITLED "ADJUSTMENTS TO PARENTAL CARE BY THE EUROPEAN STARLING (*STURNUS VULGARIS*): THE EFFECT OF FEMALE CONDITION" BE ACCEPTED AS FULFILLING PARTIAL REQUIREMENTS FOR THE THESIS IN ZOOLOGY.

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ABSTRACT

Every organism has limited energy to expend on growth, personal maintenance, and reproduction. At sexual maturity, life history theory predicts a trade-off will exist between self-maintenance and investment in offspring. I examined the extent to which a decrease in female body condition affected male and female parental care in a population of European Starlings (*Sturnus vulgaris*). By clipping wing and tail feathers of females to reduce their foraging ability, I predicted female parental care would decrease, and male parental care would increase in compensation. Young raised at experimental nests during the 2002 breeding season fledged at significantly lower masses than those raised at control nests. This suggests that females compensated for their handicapped condition by decreasing reproductive energy expenditure, possibly by changing foraging strategy from prey of higher quality to prey of higher availability, or by decreasing prey load per feeding trip. Visitation rates by both parents at experimental nests tended to be slightly lower than those at control nests, though this difference was not statistically significant. Clipped females did not lose more body mass than control females during the reproductive season, indicating that females were not willing to overcompensate for the increase in cost of reproduction.

Key words: parental care, female condition, energy expenditure, life history theory, European Starling, *Sturnus vulgaris*.

INTRODUCTION

Life history theory predicts a trade-off between self-maintenance and investment in offspring for an organism to achieve maximum reproductive success. If energy and time are limited, then a parent may choose to allocate resources to self-maintenance and predator avoidance. This strategy could extend the reproductive life of the parent, but the little energy remaining for investment in offspring would allow only minimal parental care. Conversely, a parent may invest heavily in offspring, but the potential risks of reproduction could reduce survival (Ricklefs 2000a).

Many avian studies have investigated the trade-offs made by parents faced with increased demands on their energy during reproduction. Females of several different passerine species have been found to reduce clutch size or decrease parental care when flight feathers were experimentally removed prior to laying (Slagsvold and Lifjeld 1988; Slagsvold and Lifjeld 1990; Winkler and Allen 1995). Wright and Cuthill (1989) performed a handicapping experiment in which they added weights to the tails of European Starlings (*Sturnus vulgaris*) after laying. This resulted in a reduction in the weighted birds' parental care. The unweighted partner did not completely compensate for its partner, so the offspring suffered the costs of the manipulation. By reducing a parent's ability to care for itself and its young, these experiments show how parents allocate energy expenditure between competing demands. With this information, one can begin to understand the selective pressures responsible for the evolution of parental care.

I examined the extent to which a decrease in female body condition affected male and female parental care in a population of European Starlings. Female condition was reduced by decreasing her foraging ability, which I achieved by clipping wing and tail feathers. Because of high adult annual survival (Feare 1984), I predicted that a reduction in condition would result in

a corresponding decrease in investment in offspring. I also predicted that a decrease in female parental care would result in an increase in care by her male partner.

METHODS

Study site and species

The European Starling (*Sturnus vulgaris*) is an ideal species for examining trade-offs because of its success and abundance. Human disturbance has greatly increased starling habitat, as starlings often nest in man-made structures and exploit food resources found in urban and agricultural areas. Their low sensitivity to disturbance allows for experimentation without the risk of parents abandoning their young (Cabe 1993). Starlings are secondary cavity nesters and are readily attracted to nest boxes. In addition, they are highly social, so pairs will utilize nests that are in close proximity to each other (Cabe 1993).

In northern Utah, starlings typically complete two broods during the breeding season, which begins in the spring and continues through early summer. The modal clutch size is 5 eggs, and full time incubation begins the day the last egg is laid (Cavitt, pers. comm.). Incubation lasts between 11-12 days, with the female responsible for about 70% of the incubation during the day, and all of it at night (Cabe 1993). Nestlings are fed by one or both parents in the nest for 21-22 days, beginning at hatching (brood day 0), and continuing for an additional week after nest leaving.

This experiment was conducted at the Abbey of Our Lady of the Holy Trinity Monastery in Huntsville, Utah, May to July, 2002. The nest box colony consisted of 98 wooden boxes (22 cm x 23 cm x 41 cm), each with a detachable lid for easy access to the nest, and a metal, sliding trap door to facilitate capture of adults. Boxes were attached to old barns and outbuildings, as

well as fences surrounding alfalfa fields. Starlings forage for food in the highest soil layer and dense vegetation directly above it (Tinbergen 1981). The many fields surrounding the study site provided excellent foraging opportunities for this population of about 70 breeding pairs.

General procedures

Throughout the breeding season, I attempted to capture males and females for measurements and banding. I captured adults by tying fishing line to the metal trap door on the nest box, so that, when a starling entered the box, the line could be pulled, trapping the bird inside. I measured each adult's culmen length (from nares to tip), tarsus length, wing chord, tail length, and body mass. To aid in quick identification from a distance, each adult was banded with a unique combination of colored leg bands (maximum of 2 bands per leg). Each combination included one silver U.S. Fish and Wildlife Service (USFWS) band, engraved with a unique identification number.

All nest boxes were checked twice weekly for nest building activity and for determination of clutch initiation. Clutch size was assigned when two successive nest visits yielded the same number of eggs in a nest. Nests were checked daily for hatching beginning about ten days after completion of laying, and the day that the first egg in a nest hatched was designated as brood day 0. Number of young (or brood size) was recorded and the nestlings were weighed on brood days 0, 4, and 8. On day 12, nestlings were banded with one silver USFWS identification band, weighed, and wing chord and tarsus length measured. Beginning with day 14, nests were checked daily until all nestlings had left the nest.

Parents were identified and assigned to particular nests based on observations of incubation or nestling feeding. Males that did not exhibit parental care were designated to

broods if observed in nest building activities, mating displays on a particular nest box, or nest defense.

Experimental procedures

Thirty-two nests were randomly allocated to either the experimental or control treatments at hatching. Females were captured near the time of hatching (brood day 0-2) for initial weighing and handicapping. Females allocated to the experimental treatment had primaries 3, 6, and 9, secondaries 3 and 6, and retrices 3 and 6 clipped near the base. This handicap was only temporary, as clipped feathers were replaced in the pre-basic molt. All females were recaptured between brood days 12 and 18 for a second weighing to assess relative female body condition. I made three separate observations per nest, occurring on brood days 2-4, 7-10, and 17-19, to measure numbers of total visits and feeding visits by males and females. Each observation lasted from 60-120 min, and was done by either personal observation or recorded with a video camera.

Statistical analyses

I performed parametric analyses, except when assumptions of statistical tests could not be met. I analyzed mean brood mass and female mass loss during the nestling period to determine if foraging adjustments were made. I also tested for differences between control and experimental broods in number of fledged young, brood survival, and length of the nestling period. To assess any behavioral adjustments made to parental care, I examined the effect of treatment on total nest visitations made per young by males and females.

RESULTS

Mean brood mass was significantly lower at experimental nests than controls by brood day 12 (Figure 1). A trend was observed in brood mass difference between treatments, beginning with no difference on day 4 ($F_{1,28} = 0.001$, $P = 0.972$), and day 8 ($F_{1,24} = 1.060$, $P = 0.313$), and finally, a significant difference on day 12 ($F_{1,21} = 6.763$, $P = 0.017$). There was no significant difference between treatments in female body mass loss during the nestling period, and no significant difference was found between treatment groups in number of fledged young, brood survival, or length of the nestling period (Table 1). Twelve of the 32 nests failed at various stages of their nestling periods due to predation, abandonment, or other unknown causes. However, an equal number of nests failed in the experimental and control groups, so my treatment was not believed to increase nest failures.

ANOVA for female nest visitation rate per young per hour revealed no significant difference between treatment groups, but the mean visitation rate at experimental nests was slightly less than at control nests (Table 1). Only 14 of the 32 nests observed during the nestling period received any male parental care. Consequently, analysis of male visitation rate per young per hour was performed solely on those nests where males were observed caring for the young at least once. Males that participated in parental duties did so significantly less at experimental nests compared to control nests on brood day 9 (Figure 2; Mann-Whitney U-test; $U = 24.000$, $P = 0.028$).

DISCUSSION

Condition of young

Young raised by handicapped females fledged at a significantly lower mass than those raised in control nests, but I found no difference between treatments in female body mass. This suggests that handicapped females passed the consequences of their decreased condition onto their young, rather than suffering the consequences themselves. Since no significant difference was found between treatments in the rate of nest visitation by the female, the decrease in brood mass may be due to a change in foraging strategy by the parents as a result of our manipulation of the female. It is unknown whether this brood mass difference could be due to a decrease in prey load per feeding trip, a change in prey type, or some combination of both.

Wright et al. (1998) found that starlings often make trade-offs from "quality" (more nutritious prey) to "quantity" (more abundant prey) when presented with the difficulty of feeding an artificially enlarged brood. This could explain the brood mass difference in my experiment, if the parents were choosing less nutritious, more abundant prey to make up for the female's increased energy costs. A switch from quality food to quantity food would be consistent with my results of no difference in brood survival and number of fledged young. The effect of the trade-off would take some time to manifest itself, first in the form of decreased brood mass as the nestling period came to an end, and eventually resulting in decreased survival for the young. To determine if this were the case, I would need to investigate the condition and survival of fledglings after nest leaving.

Male parental investment

Only half of the nests received any feeding visits by males, and I found that males who were caring for their young were doing so at lower rates at experimental nests versus control. A female handicapping experiment conducted on three tit (*Parus* spp.) found that males were not willing to invest more in parental care after the handicapping of their mate, possibly because the mate was considered "low quality" (Slagsvold and Lifjeld 1990). In contrast, Wright and Cuthill (1989) observed a slight increase in parental care by males after adding weights to the tails of the birds' mates, though this did not completely compensate for the reduction in care by the females. It is possible that in a population in which males were primarily monogamous and provided almost half of the total parental care (e.g. Wright and Cuthill 1989) handicapped females could decrease visitation rate with some assurance that their partners would compensate by increasing their parental care. In this population, females may have adopted a different strategy due to the unpredictability of male participation in parental duties. Female visitation rate remained the same, but personal energy expenditure in parental care was still reduced elsewhere, as evidenced by the decreased brood mass at experimental nests.

The European Starling is facultatively polygynous, with little to no parental care invested by males in the broods of secondary females, and decreased male help for the broods of primary females, compared to the investment made by monogamous males (Sandell et al. 1996). There is also a large amount of variation in the extent to which polygynous males of a single species will participate in the feeding of their young (Sandell et al. 1996). Polygyny has been observed in this population, but future investigation is needed to determine its extent. In this study, the identity of only 9 males out of 32 pairs was positively known, so it is conceivable that polygyny was an important factor in the large variation of male parental care observed. Also, males

presented with the opportunity to attract additional females will often invest less in their current broods (Sandell et al. 1996). It is possible that as the breeding season neared its end, males in this population no longer had enough time or resources to feed nestlings and attract additional mates, so they may have opted out of parental duties in favor of soliciting extra-pair copulations.

Female parental investment

Contrary to expectation, I found no difference in nest visitation rate between treatment and control females. It is possible that females do not work at their maximum capacity, to allow for environmental unpredictability. Therefore, any change would not threaten survival and future reproduction (Drent and Daan 1980). Handicapped females could have adjusted their energy expenditure to come nearer to their maximum capacity, but as it was only a short-term adjustment, personal survival and current reproduction were not severely affected.

Other similar studies have found that handicapped females of several different passerine species lost more mass during the nestling period than controls, indicating that they bore the brunt of their handicap rather than passing the costs onto their offspring (Slagsvold and Lifjeld 1988; Slagsvold and Lifjeld 1990; Winkler and Allen 1995). In this study, clipped females did not lose more body mass than control females, so the results suggest that females were not willing to pay the price for the increase in cost of reproduction. With a decrease to body condition, females that invest heavily in their current offspring may jeopardize their future reproductive success (Ricklefs 2000b). European Starlings have relatively high lifetime reproductive success, due to high annual survival, flexibility of mating systems, and the production of two broods per female during each reproductive season (Feare 1984). Therefore,

future reproductive opportunities may still be available to females with lowered body condition by investing more in themselves than current offspring.

ACKNOWLEDGEMENTS

We would like to thank the 2002 starling crew for help with data collection: N. Francis, J. Johanson, J. Jones, K. Lyngle, T. Ray, A. Sedrick, N. Summers, and L. Colton. Also, we are grateful for the generous grant provided by the Hemingway Foundation in support of Weber State University's Summer Undergraduate Research Experience. Finally, we would like to thank the Monks of the Abbey of Our Lady of the Holy Trinity Monastery for the use of their lands.

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Table 1. Effects of treatment on several different variables during the nestling period.

	TREATMENT		CONTROL				
VARIABLE	Mean ± SE	*n*	Mean ± SE	*n*	F	P	$df_{model, error}$
Female mass loss (g)	5.167 ± 0.427	9	6.011 ± 1.229	9	38.000[d]	0.825	1,16
Number of fledged young[a]	3.500 ± 0.401	10	3.800 ± 0.359	10	0.310	0.584	1,18
Brood survival[b]	0.972 ± 0.019	12	0.923 ± 0.033	11	49.000[d]	0.175	1,21
Length of the nestling period (days)[c]	21.444 ± 0.444	9	21.000 ± 0.394	10	0.564	0.463	1,17
Female nest visits per hour							
Brood day 3	1.082 ± 0.177	12	2.014 ± 0.660	12	2.214	0.151	1,22
Brood day 9	2.123 ± 0.439	12	2.599 ± 0.381	11	0.659	0.426	1,21
Brood day 18	2.372 ± 0.712	8	2.274 ± 0.379	11	0.017	0.897	1,17

[a]Successful nests only

[b]Number of young on day 12 / day 4; means were arcsin transformed for analysis

[c]Hatch day to fledge day

[d]Mann-Whitney U value

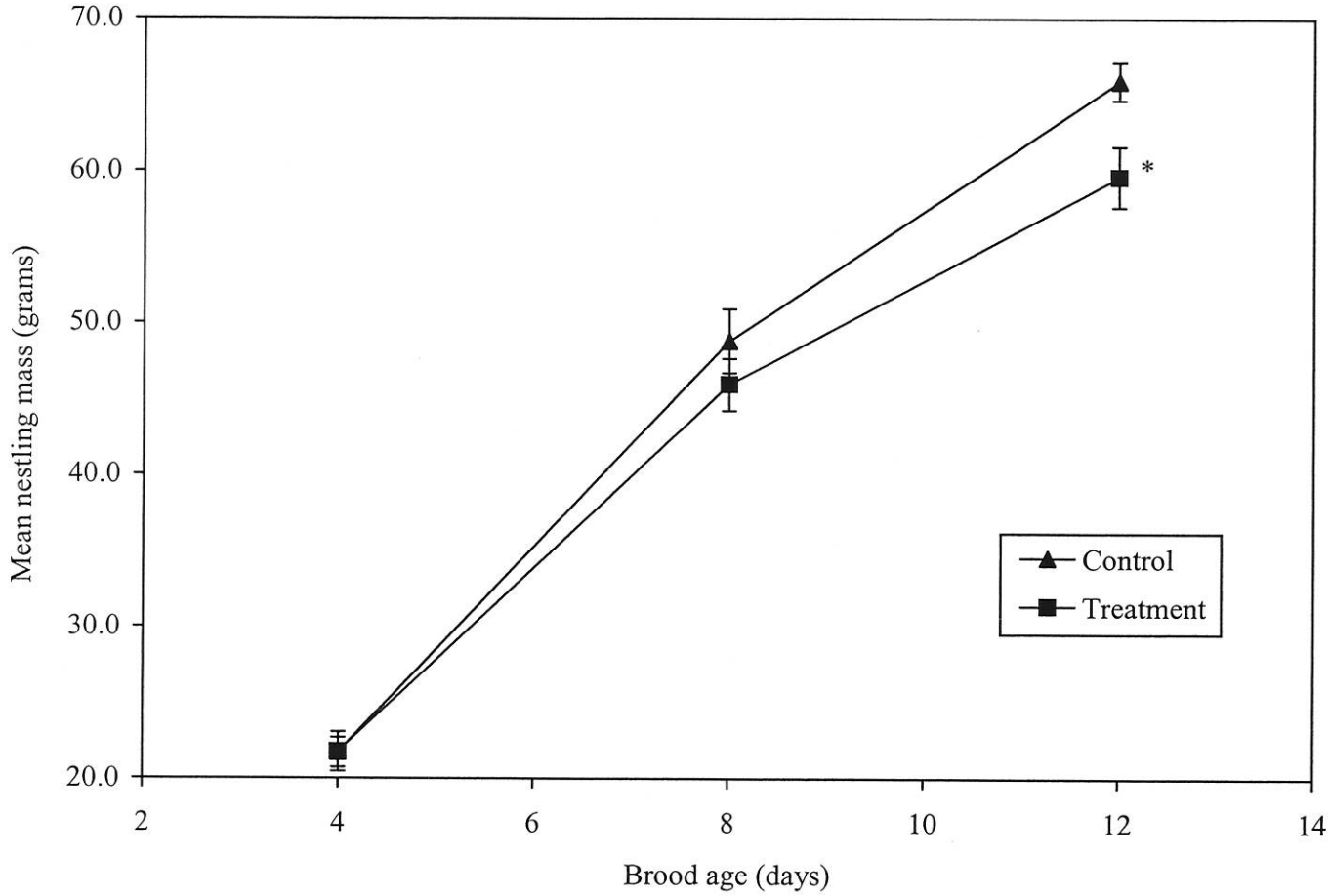

Figure 1. Mean (±SE) nestling mass at treatment nests and control nests during the nestling period (*P < 0.05).

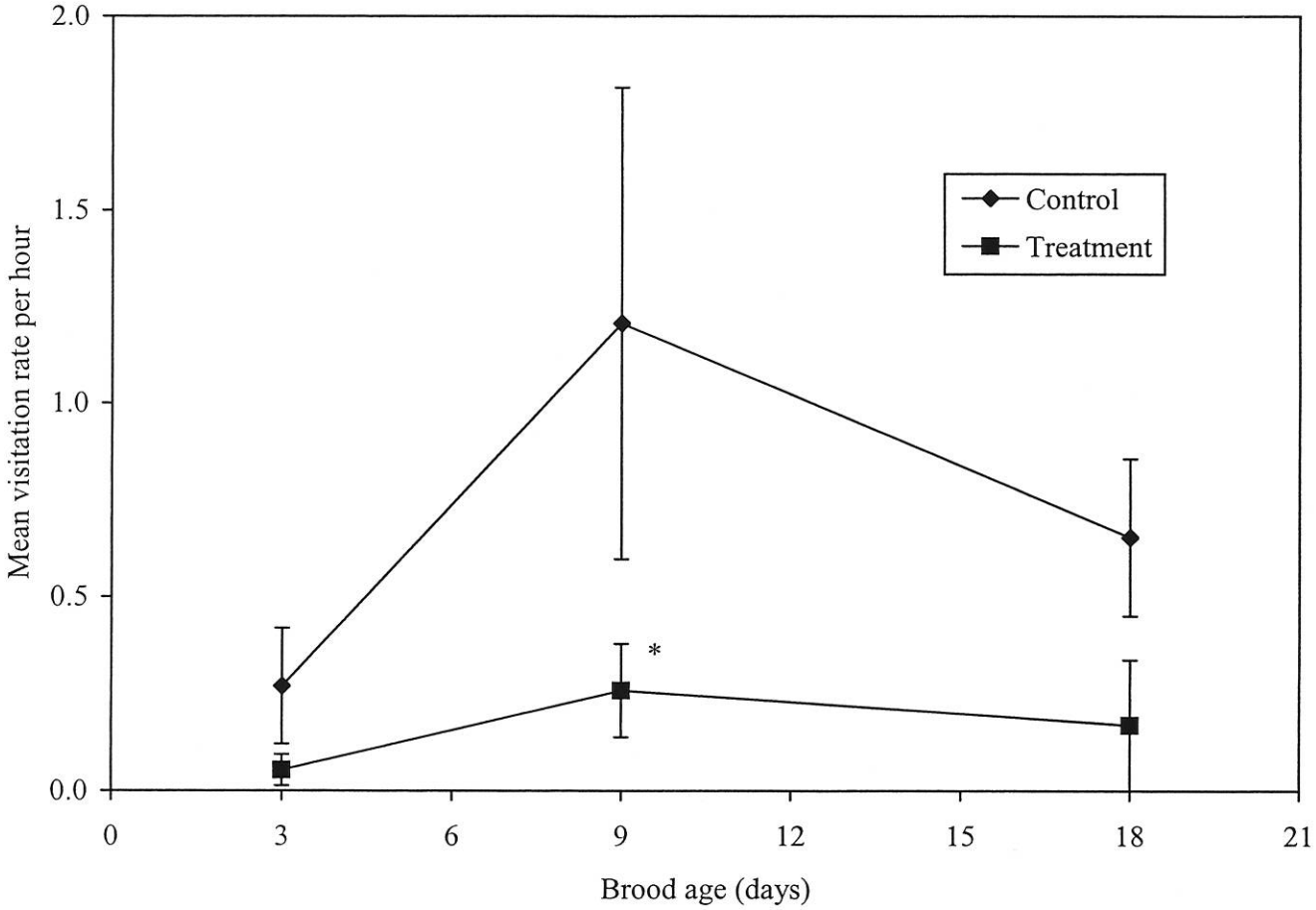

Figure 2. Mean (±SE) nest visitation rate per hour of males at treatment nests and control nests during the nestling period (*P < 0.05).