ORIGINAL ARTICLE

Fitness consequences of male provisioning of incubating females in a desert passerine bird

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Abstract Male provisioning of incubating females can increase reproductive success by maintaining physiological condition of females and consistency of incubation. The effects of male provisioning on the maintenance of incubation temperature and embryo development should be particularly pronounced in environments where ambient temperature exceeds the tolerance of unincubated eggs and where consistency of female incubation might be particularly important for hatching success. Here, we investigated the reproductive consequences of incubation feeding in a desert population of House Finches (*Carpodacus mexicanus*) in southwestern Arizona. We found that greater nest attentiveness by females was related to higher minimum incubation nest temperature, that in turn was closely associated with hatching success. Only 44% of males regularly provisioned their incubating females. Although provisioned females maintained higher incubation temperature and took fewer incubation breaks than non-provisioned females, overall, male provisioning did not influence incubation dynamics or hatching success. Further, a male's incubation feeding rate did not correlate with male provisioning of nestlings. These results corroborate the finding that, in male House Finches, neither provisioning of incubating females nor pre-incubation courtship feeding are associated with increases in circulating pituitary prolactin—the hormone regulating male provisioning of nestlings. We suggest that incubation provisioning by male might be a component of pair maintenance behavior
and that variation in male incubation behavior is best understood in relation to asymmetries in residual reproductive values between the mates.

Introduction

Male provisioning of incubating females varies widely both among and within species (Silver et al. 1985). Variation in male provisioning rates is thought to reflect a compromise between the costs of provisioning, such as increased predation risk, energetic limitations, and missed mating opportunities (Skutch 1985; Smith 1995; Martin and Ghalambor 1999; Conway and Martin 2000; Cresswell et al. 2003), and its benefits such as pair bond maintenance, mate guarding, and greater incubation efficiency (Lack 1940, 1968; Martin 2002; Chalfoun and Martin 2007). In particular, incubation feeding can increase nest attentiveness by reducing the amount of time the female spends foraging off the nest (Hatchwell et al. 1999; Jawor and Breitwisch 2006). When greater nest attentiveness is associated with higher consistency of egg temperatures, it can lead to greater hatching success and fewer developing abnormalities in embryos (Webb 1987; Deeming 2002; Olson et al. 2006).

Greater nest attentiveness and egg temperature consistency is particularly important in environments or times of season where ambient temperature exceeds the limits of temperature tolerance of unattended nests (e.g., Badyaev et al. 2003; Martin et al. 2007). In such environments, male provisioning of females can play a crucial role in the maintenance of egg temperature and hatching success (e.g., Lyon and Montgomerie 1987; Badyaev and Ghalambor

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2001). Further, birds nesting in hot desert environments are under additional risk of hyperthermia, and incubation behavior in such environments includes nest shading and maintaining a lower than ambient core body temperature through evaporative cooling (Walsberg 1983; Stoleson and Beissinger 1999; Brown and Downs 2002; Amat and Masero 2004). Heating and cooling the nest requires the female to be present on the nest, yet thermoregulatory behaviors are constrained by the necessity of food acquisition, the risk of dehydration, predation, and pair maintenance, and some of these costs might be lessened by male provisioning.

We investigated the reproductive consequences of male provisioning of incubating females in a native population of House Finches (*Carpodacus mexicanus*) in the Sonoran desert of southwestern Arizona, US. In House Finches, only the female incubates, but males often feed incubating females on the nest, although the extent of male provisioning varies widely both within and across populations (Hill 1991, 1993, 2002; Badyaev and Hill 2002; Duckworth et al. 2003; McGraw and Hill 2004). Here, we first show that incubation behavior strongly determined nest temperature during incubation and that maintenance of nest incubation temperature was closely associated with hatching success. Second, we examine the prevalence of male feeding of incubating females in this population and the contribution of male provisioning of incubating females to incubation behavior and hatching success.

Methods

House Finches were studied in a resident population in southwestern Arizona since 2002 and data for this study were collected in 2004–2005. Birds were trapped year round and marked with a unique combination of one aluminum and three colored plastic rings. All nesting and most pairing affiliations were known for resident birds through continuous direct observations and videotaping, and confirmed by genetic paternity analyses (see Badyaev and Vleck 2007 and Oh and Badyaev 2008 for details of the field protocol). Nests used in this study ($n = 114$) were followed from the onset of building, and male provisioning was assessed through monitoring during incubation and nestling periods. Hatching success was measured as the proportion of eggs that hatched out of the total clutch.

Provisioning rates during incubation (both on and near nests) and nestling period were recorded during 90–120 min observations with a combination of digital video cameras mounted near the nest site and by observers on the ground, and repeated observations of the same nests on consecutive days were averaged for the analyses.

Incubation temperature and attentiveness were recorded with Thermochron iButtons (Maxim Integrated Products, Sunnyvale, CA) installed in each nest at the commencement of nest building. iButtons recorded temperature immediately under eggs (hereafter nest temperature) every 5 min during the first half (5–7 days) of the incubation period. Onset of incubation and off-bouts were easily identifiable from the thermoprobe recording by at least a 2°C drop between contiguous sampling points. Off-bout numbers (total) and mean off-bout duration per hour were calculated for the entire early incubation period.

Only first breeding attempts from a female were used in the analyses, and variation due to nest initiation date (and thus seasonal changes in ambient temperature) was controlled in general linear models. Groups of provisioning and non-provisioning males were compared with non-parametric Mann–Whitney U test and in general linear models. Transformations were performed as necessary to meet assumptions of normality and equality of variance; the rate variables were arcsine-transformed and linear data were log-transformed.

Results

Nest temperature over the course of incubation averaged 32.03 ± 3.21°C (SD) ($n = 78$ nests); during off-bouts, the minimum temperature (T_{min}) cooled to 10.02°C (mean $= 19.54 \pm 5.66$°C) early in the season and reached the maximum temperature (T_{max}) of 45.0°C later in the season (mean $= 37.91 \pm 2.74$°C). The range of nest temperatures fluctuated between 10.0 and 31.5°C (mean 18.6 ± 4.9°C). During the first 5 days of incubation, females spent $77 \pm 9\%$ (42–93%) of time on the nest, taking on average 51.79 ± 23.67 off-bout breaks, that varied in duration from 12.42 to 48.13 min (mean $= 23.83 \pm 8.50$) and were confined to the daylight hours. Females that took shorter off-bouts maintained higher and more consistent incubation temperature (Fig. 1) while greater number of off-bouts was associated with lower minimum temperature and more variable nest temperature (Fig. 1). Forty-two of 75 males (56%) did not provision their incubating females, while provisioning males averaged 0.89 ± 0.37 visits/h.

Overall, the rate of male provisioning of incubating females was not associated with nest temperature, off-bout number or duration (Fig. 2). However, provisioned females maintained higher incubation temperature (Fig. 2a, insert) and took fewer off-bout breaks (Fig. 2b, insert) than non-provisioned females. Hatching success averaged $87 \pm 19\%$ and did not vary with male incubation provisioning or off-bout duration, but positively varied with minimum nest temperature during incubation and with number of

Fig. 1 Partial regression plots illustrating the relationship between incubation off-bout number and off-bout duration and **a** average nest temperature, **b** maximum nest temperature, **c** minimum nest temperature, and **d** nest temperature range during incubation period of desert House Finches (*Carpodacus mexicanus*). b_{ST} are standardized regression coefficients from multiple regression. Analyses control for the effects of nest initiation date
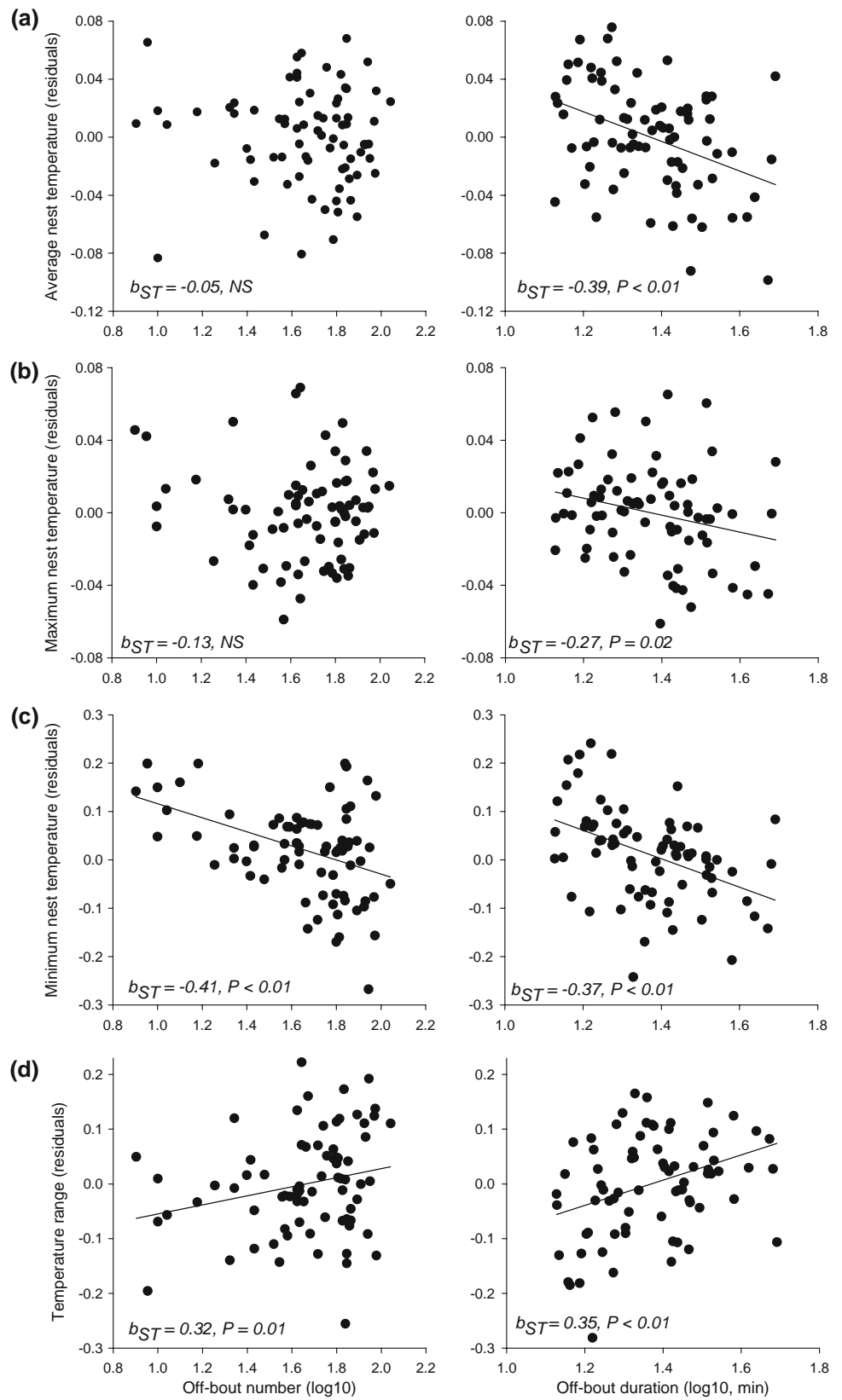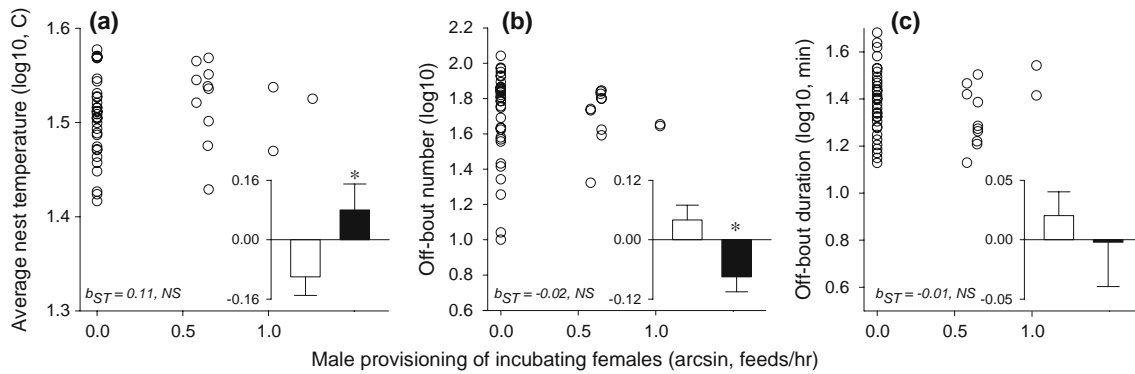
Fig. 2 Partial regression plots show consequences of male provisioning of incubating females for **a** average nest temperature, **b** off-bout number, and **c** off-bout duration. Analyses control for the effects of nest initiation date. *Inserts* show residual mean ± SE for non-provisioning males (*white bars*) and provisioning males (*black bars*) controlling for the effects of nest initiation date. *Asterisks over bars* show significant difference in means between the two groups with Mann–Whitney *U* tests ($P < 0.05$)

Fig. 3 Partial regression plots illustrating the relationship between hatching success and male incubation provisioning, nest temperature (only minimum temperature is included here based on Fig. 1), off-bout number and duration during incubation in desert House Finches. b_{ST} are standardized regression coefficients
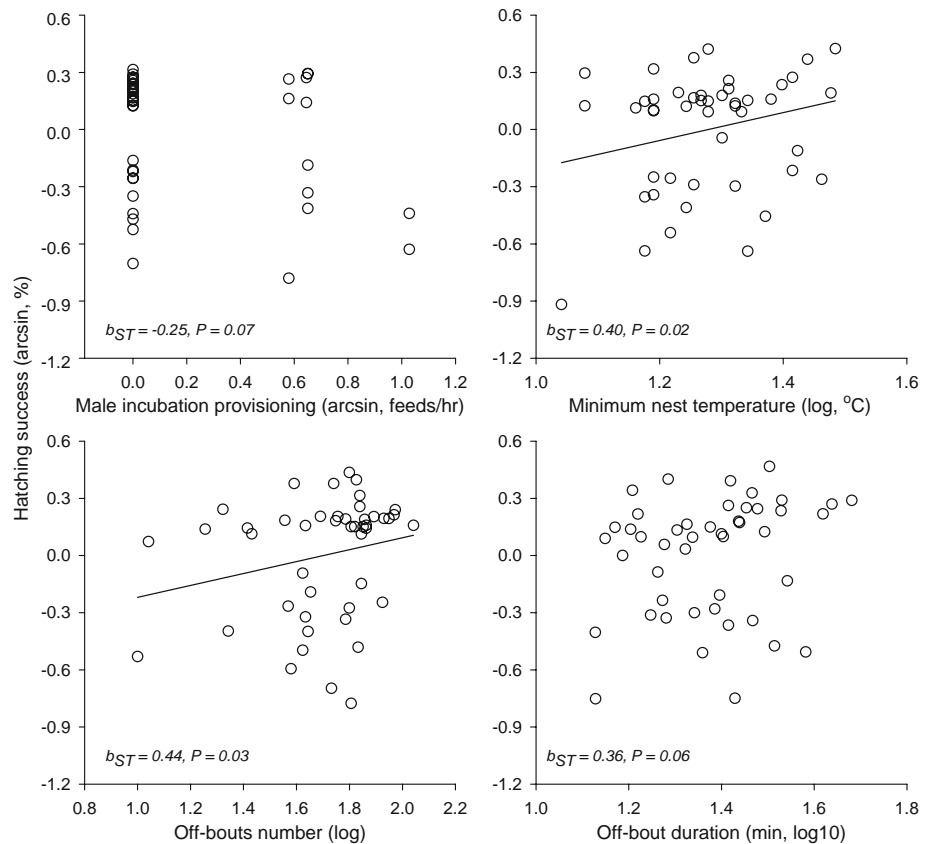
off-bouts (Fig. 3). Male provisioning of the female during incubation was not a significant predictor of male provisioning of nestlings (Fig. 4), and provisioning and non-provisioning males did not differ in the rate at which they feed their nestlings (Fig. 4 insert; $\chi^2 = 0.74$, $P > 0.1$). Fifteen out of 75 (20.3%) males did not provision nestlings and 6 males out of 75 (8%) provisioned neither their incubating females nor nestlings.

Discussion

Male provisioning of incubating females can have important consequences for the maintenance of pair bond and incubation temperature and, thus, has received considerable attention in the studies of life history evolution and sexual selection (Ricklefs 1993; Black 1996; Deeming 2002; Martin 2002). In environments where ambient
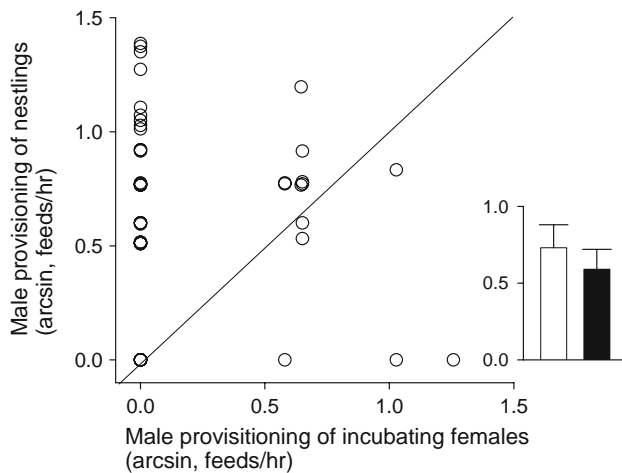
Fig. 4 Relationship between male provisioning of incubating females and nestlings ($b = -0.07 \pm 0.18$, $t = -0.41$, $P = 0.67$). *Line* is a diagonal, i.e., equal provisioning of incubating females and nestlings. *Insert* shows mean $\pm$ SE rate of male nestling provisioning by males that did not provision (*white bar*) or provisioned (*black bar*) their females during incubation

temperatures exceed that tolerated by unattended eggs, female incubation consistency is particularly important and may be enabled by male provisioning on the nest (Lyon and Montgomerie 1987; Duckworth 2006). However, these environments can also favor close coordination of physiology and behaviors of the mates, and male provisioning of incubating females can play a significant role in this process (Lyon et al. 1987; Badyaev 1997). Understanding the relative contribution of pair maintenance versus actual female incubation provisioning by male feeding is important—whereas some studies consider incubation feeding a part of paternal care and view incubation provisioning as a preview of nestling feeding, others suggest that incubation feeding is a component of pair maintenance behaviors, especially in species where male's subsequent provisioning of nestling is important for reproductive success. For example, in the House Finch—a species that nests in loosely associated colonies—the period of incubation provisioning coincides with the peak of extra-pair opportunities, and incubating female begging behavior is influenced more by the presence of fertile females in the nest vicinity than by the time since the last incubation feeding (Jonart et al. 2007; Lindstedt et al. 2007). Thus, to uncover the proximate targets of natural selection on male incubation provisioning, it is important to establish whether male incubation provisioning enables consistent incubation, whether it is linked to variation in hatching success, and whether the rate of incubation provisioning is related to male's subsequent provisioning of nestlings.

Our study of desert House Finches suggests that male provisioning of incubation females is only indirectly related to incubation consistency, hatching success, and future

nestling provisioning, but instead might represent a pair-coordination behavior. First, although longer off-bouts were associated with lower incubation temperature (Fig. 1)—the parameter linked to lower hatching success (Fig. 3)—variation in off-bout duration itself was not related to hatching success (Fig. 3). Further, the number of off-bouts, although related to the temperature to which the nest cooled during female absence (Fig. 1c) and nest temperature consistency (Fig. 1d) was nevertheless *positively* associated with hatching success. Because females take more off-bouts when not fed by their males (Jonart 2002), a greater number of shorter off-bouts (that only minimally affect average incubation temperature; Fig. 1) might represent greater foraging by these females and thus higher condition and greater overall nest attentiveness.

Second, although females that were fed by their males maintained higher incubation temperature and took fewer incubation breaks than females that were not fed (see also Lifjeld and Slagsvold 1986; Hatchwell et al. 1999), male provisioning was not associated with hatching success (Fig. 3; see also Jawor and Breitwisch 2006). If the amount of food transferred to incubating females is not sufficient to compensate for the amount of food a female can acquire by self-foraging, then fewer incubation off-bouts might be associated with off-bouts of greater duration (Fig. 1) or poorer female condition during incubation, corroborating the link between more frequent female off-bouts and greater hatching success found in this study (Fig. 3). Further, only the lowest temperature to which the nest cools during off-bouts was associated with hatching probability (Fig. 3), explaining why the variation in average incubation temperature linked to male provisioning (Fig. 2a) was not an important determinant of hatching success.

Third, male provisioning of incubation females did not reliably indicate male's subsequent provisioning of nestlings (Fig. 4; see also Jawor and Breitwisch 2006)—most males that did not provision their incubating females nevertheless fed their nestlings, and the rate of male provisioning of nestlings did not differ between males that fed their incubating female and males that did not (Fig. 4 insert). These results corroborate the finding that, in the House Finch, neither male provisioning of incubating females nor pre-incubation courtship feeding are associated with increase in circulating pituitary prolactin—the hormone regulating male provisioning of nestlings in this species (Duckworth et al. 2003; see Vleck 2002 for review). Experimental blocking of prolactin production by implants of bromocryptine did not influence the rate of incubation feeding by males, whereas it prevented feeding of nestlings (Badyaev and Duckworth 2005). Distinct effects of prolactin might be associated with its effect on crop lining (Buntin 1996; Vleck et al. 2000)—in House Finches nestling provisioning by males involves

transportation of significant amounts of food in the crop whereas fewer food portions are transferred to incubating females (personal observation; see also Nolan et al. 2001).

Taken together, these results suggest that male provisioning of incubating females and male provisioning of nestlings can be different processes and should be considered in a wider life history framework (Nisbet 1973; Niebuhr 1981; Gauthier-Clerc et al. 2001; Jawor and Breitwisch 2006; Klatt et al. 2007). In a northern House Finch population, provisioning of incubating females was associated with limited breeding opportunities experienced by the provisioning males and was particularly prevalent in pairs of first-breeding individuals (Badyaev and Hill 2002; see also McGraw et al. 2001; McGraw and Hill 2004). Thus, the lack of effect of male incubation provisioning on hatching success found in this study (Fig. 3) might be confounded by age- and experience-related variation in reproductive performance. Similarly, other studies proposed that incubation feeding can be a manipulative behavior induced by females in order to lower their costs of reproduction costs, assess mate quality (Lyon and Montgomerie 1985), or limit extra-pair matings (Smith 1980; Lindstedt et al. 2007). Our study suggests that the analyses of variation in incubation provisioning rate might be particularly fruitful in a framework that explicitly considers asymmetries in residual reproductive values and current mating opportunities between the mates.

Zusammenfassung

Fitnesskonsequenzen der Versorgung brütender Weibchen durch die Männchen bei einem Wüsten bewohnenden Sperlingsvogel

Das Versorgen brütender Weibchen durch die Männchen kann den Fortpflanzungserfolg erhöhen, indem es den physiologischen Zustand der Weibchen und die Kontinuität des Brütens aufrechterhält. Die Effekte der Versorgung durch die Männchen auf die Aufrechterhaltung der Bebrütungstemperatur und die Embryonalentwicklung sollten besonders in solchen Umwelten ausgeprägt sein, in denen die Umgebungstemperatur die Toleranz unbebrüteter Eier überschreitet und in denen die Kontinuität der Bebrütung durch das Weibchen besonders wichtig für den Schlüpferfolg sein dürfte. Hier haben wir die reproduktiven Konsequenzen des Versorgens während der Bebrütung in einer Wüstenpopulation von Hausgimpeln (Carpodacus mexicanus) in Südwestarizona untersucht. Wir fanden, dass eine stärkere Anwesenheit von Weibchen am Nest mit einer höheren Minimumtemperatur im Nest während der Bebrütung in Zusammenhang stand, welche wiederum eng mit dem Schlüpferfolg assoziiert war. Nur 44% der Männchen

versorgten regelmäßig ihr brütendes Weibchen. Obwohl versorgte Weibchen höhere Bebrütungstemperaturen aufrechterhielten und weniger Bebrütungspausen einlegten als nicht versorgte Weibchen, beeinflusste das Füttern durch das Männchen insgesamt nicht die Bebrütungsdynamik oder den Schlupferfolg. Außerdem korrelierte die Fütterungsrate eines Männchens während der Bebrütung nicht mit dem Füttern der Nestlinge durch das Männchen. Diese Ergebnisse stützen den Befund, dass bei männlichen Hausgimpeln weder das Füttern brütender Weibchen noch das Balzfüttern vor der Bebrütungsphase mit einem Anstieg des zirkulierenden Prolaktins, des Hypophysenhormons, welches das Füttern der Nestlinge durch das Männchen reguliert, in Zusammenhang stehen. Wir schlagen vor, dass das Füttern des Weibchens durch das Männchen während der Bebrütungsphase ein Teil des Paarerhaltungsverhaltens ist und dass Variation im männlichen Bebrütungsverhalten am besten in Bezug auf Asymmetrien im Restreproduktionswert zwischen den Partnern verstanden wird.

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