Morphological and genetic predictors of parental care in the North American barn swallow *Hirundo rustica erythrogaster*

Sarah E. Maguire and Rebecca J. Safran

S. E. Maguire, Dept. of Biol., Univ. of Pennsylvania, Philadelphia, PA 19104-6018, USA. – R. J. Safran (correspondence), Dept. of Ecol. and Evol. Biol., Univ. of Colorado, Boulder, CO, 80309, USA. E-mail: rebecca.safran@colorado.edu.

Sexually dimorphic traits often signal the fitness benefits an individual can provide to potential mates. In species with altricial young, these signals may also predict the level of parental care an individual is expected to provide to shared offspring. In this study, we tested three hypotheses that traditionally relate sexually dimorphic traits to parental care in two populations of North American barn swallows *Hirundo rustica erythrogaster*. The good parent hypothesis predicts a positive relationship between an individual's ornamentation and his or her care whereas the differential allocation (more care given by individuals when paired to high quality mates) and reproductive compensation (more care given by individuals when paired to low quality mates) hypotheses predict that an individual's level of parental investment is relative to the quality of their mate. Male and female North American barn swallows have colorful ventral feathers and elongated tail streamers, but there is evidence that ventral color, not tail streamer length, predicts measures of seasonal reproductive success. Accounting for the positive correlation between within-pair feeding rates and other potentially confounding variables in all of our models, we found no support for the good parent hypothesis because in both males and females, traits shown to be under sexual selection did not predict feeding rates in either sex. However, our data reveal that male coloration, and not streamer length, predicted a female's provisioning rate to shared offspring (females fed more when paired with darker individuals) in two separate populations, supporting the differential allocation, but not the reproductive compensation hypothesis. Because genetic traits have also been shown to affect parental investment, we evaluated this variable as well and found that a male's paternity did not have significant effects on either male or female feeding rates. Overall, our results suggest that females do not pair with darker males in order to gain direct benefits in terms of his expected levels of parental care to shared offspring, but do themselves invest greater levels of care when paired to darker males. Further, our results are consistent with previous studies which suggest that ventral feather color, not streamer length, is a target of sexual selection in North American populations of barn swallow because females invested more in their offspring when paired to darker mates.

Theory predicts that traits under sexual selection communicate information to conspecifics about an individual's quality (Andersson 1994). Especially in altricial species where biparental care is important for the survival of shared young, individuals should pay attention during mate selection to traits that could signal parental abilities. Currently, there are three hypotheses that predict the relationship between sexually dimorphic traits and parental care. The good parent hypothesis predicts a positive association between phenotypic expression and care, where individuals with the most exaggerated traits (and thus, presumably of higher quality) invest more in offspring (Hoelzer 1989; Table 1). According to the good parent model, sexual signals are used to predict the amount of parental care that individuals should provide to shared offspring. Two additional and commonly tested models of parental care that are related to sexual signals are the differential allocation (Burley 1986) and reproductive compensation (Saino et al. 2002, Bolund et al. 2009, Harris and Uller 2009) hypotheses. The most general

prediction of the differential allocation hypothesis (Burley 1986; Table 1) is that individuals respond to their partners' sexual signals and will provide more parental care to attractive mates, regardless of their mate's contributions. The reproductive compensation hypothesis is related to differential allocation and explains patterns of parental investment in which individuals paired to low quality mates must compensate for poor care by these individuals (Saino et al. 2002, Bolund et al. 2009, Harris and Uller 2009).

Recently, the good parent (Hoelzer 1989; Table 1) and differential allocation (Burley 1986; Table 1) hypotheses have come under scrutiny because empirical data have reached conflicting conclusions as to how individuals should respond to their own or their mates' attractiveness. For example, research testing the good parent hypothesis (Hoelzer 1989; Table 1) has found inconclusive evidence, including positive (e.g. Hill 1991, Linville et al. 1998), negative (e.g. Sundberg and Larsson 1994), and no relationship (e.g. Balenger et al. 2007) between sexually dimorphic traits and levels of parental investment.

Table 1. Predictions of the good parent, differential allocation, and reproductive compensation hypotheses and results of our study.

Hypothesis	Is parental care relative to self or mate quality?	Predicted pattern	Results
Good parent	Self	Attractive individuals provide more care.	No pattern in either males or females.
Differential allocation	Mate	Individuals paired to attractive partners provide more care, and in some cases this is a consequence of or allows for the attractive mates to reduce parental behaviors.	Females paired to males with darker plumage increased care.
Reproductive compensation	Mate	Individuals paired to low quality partners must provide more care to compensate for reduced care by their mates.	No pattern in either males or females.

Similarly, tests of the differential allocation hypothesis in several species have shown variable results (Sheldon 2000), including scenarios where individuals adjusted parental investment (Limbourg et al. 2004, Gilbert et al. 2006), or were unresponsive to their partners' ornamentation (e.g. Johnsen et al. 2005). Further, recent studies have found support for the reproductive compensation hypothesis (Saino et al. 2002, Bolund et al. 2009, Harris and Uller 2009), which counters the general prediction of the differential allocation hypothesis (Burley 1986; Table 1) because it stipulates that females should provide *more* resources to the offspring of males with lower, not higher, degrees of sexual signal expression. Whereas all three of these hypotheses have focused on parental care as a function of male signals, few studies have tested whether female signals are related to parental care (Linville et al. 1998, Balenger et al. 2007), warranting further examination because female traits can also be indicative of seasonal reproductive success (Safran and McGraw 2004). Because much controversy and confusion surrounds the models relating sexual signals to parental care, our objectives were to clarify and simultaneously test predictions made by the good parent, differential allocation, and reproductive compensation hypotheses (Table 1), considering signals in both males and females and controlling for additional factors that are likely to explain patterns of parental care, including a male's paternity.

A male's paternity represents the product of both male and female reproductive decisions. It is therefore a possibility that members of each sex vary their parental investments according to these reproductive outcomes. Currently, there is support that males adjust care according to their parentage in studies of birds (e.g. Dixon et al. 1994, Weatherhead et al. 1994, Chuang-Dobbs et al. 2001) and non-bird species (fish: Neff and Gross 2001, Neff 2003, Rios-Cardenas and Webster 2005, insects: Hunt and Simmons 2002, primates: Buchan et al. 2003). However, it is currently unknown whether females vary their parental investment according to the proportion of their social mates' genetically related offspring within a brood. While it seems unlikely that females would respond to the paternity allocation of their brood *per se*, selection should favor individuals who adjust to the investment patterns of their mates (Johnstone and Hinde 2006). Thus, if males alter parental efforts according to their parentage, this might affect the amount of parental care contributed by their social mates.

In the following correlational study, we used morphological, genetic, and behavioral data from two wild populations of North American barns swallow *Hirundo rustica erythrogaster* to examine the predictors of parental care. The barn swallow is a sexually dimorphic passerine in which both sexes exhibit variation in plumage color and tail streamer length (Safran and McGraw 2004). In addition, both European and North American sub-species of barn swallows exhibit bi-parental care (Møller 1994a) and extra-pair copulations are common (e.g. Smith et al. 1991, Møller and Tegelström 1997, Saino et al. 1997, Kleven et al. 2006, Neuman et al. 2007). Previous research in a North American population of this species identified that melanin-based ventral coloration (McGraw et al. 2004, 2005), not tail streamer length, is correlated with patterns of pairing as well as apparent and genetic measures of seasonal reproductive success (Safran and McGraw 2004, Safran et al. 2005, Neuman et al. 2007), with males of darker feather color receiving greater paternity from their mates (Safran et al. 2005). However, tail streamers are also sexually dimorphic and are known sexually selected signals of quality in European populations (e.g. Møller 1988, 1992a, Saino et al. 1997, Møller et al. 1998), and possibly North American populations as well (Kleven et al. 2006). In addition, several European studies have found that tail streamer expression influences levels of parental investment (Møller 1992b, 1994b, de Lope and Møller 1993, Cuervo and Møller 2006). As such, we explore the parental care outcomes as a function of both of these traits in addition to genetic measures of paternity.

Materials and methods

We studied two populations of barn swallow from May through August in Tompkins County, New York (42° 30′N, 76° 28′W) in 2002, and in Mercer County, New Jersey (40° 37′N, 74° 67′W) in 2007. The New York population consisted of 11 breeding sites ranging from 1 to 35 pairs and the New Jersey population consisted of 4 breeding sites ranging from 13 to 17 breeding pairs. Our results are based on 50 h-long observation sessions of feeding rates (number of provisions/hour) at 22 different nests in New York and 105 h-long observation sessions at 36 different nests in New Jersey.

Using mist nets, we captured swallows during the first two weeks of the breeding season after pairs had formed.

We uniquely marked the tail streamers of individuals with enamel-based paints following Shields and Crook (1987). We also applied numbered aluminum rings and color bands to each individual. We then measured a variety of standard morphological variables (e.g. tail streamer length, wing length, mass). After identifying the individuals in each breeding site, we checked nests daily to determine breeding onset (date on which the first egg was laid), number of nesting attempts (1 or 2), and annual reproductive success (total number of young fledged within the season).

Plumage color measurements

Although color from regions across the ventral area of barn swallows (throat, breast, belly, and vent; Safran and McGraw 2004) is positively intercorrelated, throat coloration in males and belly color in females are most strongly correlated with measures of seasonal reproductive success (Safran and McGraw 2004). Accordingly, we analyzed provisioning rates as a function of male coloration in the throat region and female coloration in the belly region (Safran 2007, Safran et al. 2008).

To analyze color, we obtained a sample of 5–8 feathers from the throat region of males and from the belly region of females and mounted these on an index card to recreate the natural plumage appearance of the bird (Safran and McGraw 2004). We collected feather samples from all males from the New York and New Jersey study sites, and females from the New York site only. These cards were stored in the dark until plumage-color scoring. The color of feather samples was scored along three traditional axes of color (hue, saturation, and brightness) using a reflectance spectrophotometer (Colortron, Light Source, California, Hill 1998). This spectrophotometer does not quantify light in the ultraviolet range, but the range in which it does quantify color is sufficient for this species because the ventral plumage of barn swallows does not exhibit a unique ultraviolet reflectance peak (Safran and McGraw 2004). Color in each plumage region was measured two times and we averaged these scores to determine mean hue, saturation, and brightness for the throat region of male swallows and the belly region of female swallows. Color measures were significantly intercorrelated within each ventral region (all $P < 0.001$, all r between -0.67 and 0.82; throat for males, belly for females) so we devised a color-scoring scheme to summarize these three color scores within one region using principal components analysis (PCA) to collapse hue, saturation, and brightness scores within each plumage region. The first principal component (PC1), obtained by varimax rotation, for each region explained 78–65% of the variation in the color measures of male throat and belly color. We retained only PCs with eigenvalues greater than

one for these analyses (Dearborn and Ryan 2002; Table 2) and thus one PC used to define color for males and females was sufficient for further analyses. Birds with lower PC1 scores have browner (lower hue values), more saturated, and darker (lower brightness values) plumage and as such, lower color PC scores indicate color that is darker in appearance.

Paternity study – New York site

We used three polymorphic microsatellite loci to conduct microsatellite-based analyses to examine a male's paternity: HrU6, HrU7 (Primmer et al. 1995), and HrU10 (Primmer et al. 1996), two of which are hyper-variable (Brohede et al. 2002). The mean heterozygosities of these three loci were 0.92, 0.47, and 0.95, respectively, and the total probability of first-parent paternal exclusion using all three loci was 0.997 (Safran et al. 2005, Neuman et al. 2007).

For paternity exclusion analyses, we used Genemapper version 3.0, (Applied Biosystems) to determine allele size and assign genotypes for each individual at the three loci. We used CERVUS version 2.0 to calculate the exclusion probabilities for assessing parentage, and to test for the presence of null alleles (Marshall et al. 1998). Additional details about our lab methods and analyses can be found in Neuman et al. (2007).

Behavioral observations

Parental care studies were conducted in a single year at several study sites in New York (2002) and New Jersey (2007); as such, each individual in this study was observed during a single reproductive bout. Parental care by both males and females was calculated as the number of feeding visits/hour and was recorded between 07.00–18.30 h on days 1–16 of the nestling period (hatching = day one). Nests were observed one to three times in New York and three times in New Jersey during the early (d 4–5), middle (d 9–11) and late (d 13–15) parts of the nesting period. For logistical reasons, it was not always possible to standardize the time of data collection when nestling periods were highly synchronized across study sites, thus the time in which data were collected was used as covariate in all of our analyses. The duration of each behavioral observation session was one hour. Data were collected from behind a blind in the study site to minimize disturbance and was initiated only after the pair settled into a steady routine of visiting the nests and did not appear to be affected by our presence (e.g. no alarm calling). Behavioral data were collected using a standardized protocol adopted at both sites in which we calculated the number of times each parent came to feed at the nest during one hour.

Table 2. Results from principal components analysis on male and female color.

	Male throat PC1 – New York	Male throat PC1 – New Jersey	Female belly PC1 – New York
Explained variance	64.14	65.19	78.19
Eigenvalue	1.92	1.95	2.34
Hue	0.59	0.64	0.57
Saturation	−0.45	−0.34	−0.57
Brightness	0.66	0.67	0.59

Statistical analysis

We used mixed models with restricted maximum likelihood in SAS 9.1 (SAS Institute) to examine the relationship between the rate at which parents fed their nestlings and morphological traits, paternity, time of the behavioral observation, and the rate at which their partners provisioned. Models were run using multiple uncorrelated variables in relation to parental feeding rates. Because of their potentially confounding effect on our analyses and due to structure of our data collection (e.g. multiple nests within one breeding site), such analysis included nestling age, 'nest,' 'breeding site,' and 'brood size' as random effects. Using 'site' as a random effect controlled for repeated observations (breeding pairs) within the same site and using 'nest' controlled for the non-independence of repeated observations (multiple observations of feeding rates in the same nest during the different nestling periods) of the same pair. When statistically significant, random effects are listed in the "Results" section, unless otherwise noted.

Because male paternity is correlated with ventral color (Safran et al. 2005), it was not possible to include both effects of paternity and ventral color in the same model to examine their role simultaneously on feeding rates. As such, we used two separate analyses to assess the role of paternity on both male and female feeding, respectively, while retaining partner investment as a covariate. Further, because males and females pair assortatively by ventral color (Safran and McGraw 2004), we could not include both male and female morphological features in the same model in order to simultaneously examine their effects on parental care. As a consequence, we constructed separate models to examine male and female parental care responses in relation to aspects of a female's morphology (streamer lengths and color).

Results

Good parent hypothesis

The good parent hypothesis predicts that parental feeding rates are correlated with morphological signals of quality (Table 1). However, contrary to the predictions of this hypothesis, we found no significant association between a male's sexually dimorphic traits (color or streamer length) and his parental care (Table 3) nor a female's sexually dimorphic traits (color or streamer length) and her parental care (Table 4) in both our New York and New Jersey study sites.

Differential allocation/reproductive compensation hypotheses

In agreement with the general prediction made by the differential allocation hypothesis (Table 1), our data from both New York and New Jersey showed that females provisioned nestlings at a significantly higher rate when paired to naturally darker males (Table 5; Fig. 1a, b). This increase in female care was not a response to a reduction of male care (we found no differences in male care as a function of color; Table 3) and as such provides no support for the reproductive compensation model.

Unlike European populations of barn swallows (e.g. Møller 1992b, 1994b, de Lope and Møller 1993; but see Møller 1988, 1989, 1990, Cuervo and Møller 2006), variation in male streamer length did not influence the feeding rate of his female partner (Table 5, Fig. 2a, b).

We found no evidence that males provisioned nestlings differently as a function of their partners' streamer lengths or color (Table 4). Instead, only females differentially allocated care in relation to their mate's quality, and specifically fed at higher rates when paired to a darker male in two separate populations.

Parental care as predicted by paternity, partner behavior and sex

We did not find significant evidence that paternity affected male feeding (Mixed model: paternity $F_{1, 13} = 2.43$, $P > 0.14$; female feeding rate $F_{1, 43.8} = 11.52$, $P < 0.01$; random effects = site, nest, brood size, nestling age; Fig. 3a). Additionally, we did not find a difference in female feeding rates as a function of the paternity (Mixed model: paternity $F_{1, 18.8} = 3.47$, $P = 0.07$; male feeding rate $F_{1, 45.9} = 21.59$, $P < 0.001$; random effects = site, nest, brood size, nestling age; Fig. 3b).

In both populations, partner feeding was positively correlated with the feeding rate of the mate (Table 3, 4 and 5; Fig. 4a, b), suggesting that males and females are coordinated in their care of shared offspring. Interestingly, in both NY and NJ the slope of the relationship between male and female care was positive, but less than 1 suggesting that females increased their feeding rates to a greater extent than their male partners even after we accounted for differences in nestling age and brood size.

Within pairs, overall parental feeding rates over the course of the nestling period did not vary significantly as a function of sex in New York or New Jersey. In New York, we did not find significant differences between male and

Table 3. No evidence of support for the good parent hypothesis in males. Mixed models of male feeding rates (number of feeding visits/hr) in relation to male sexually dimorphic traits, partner feeding rates, and time in which data were collected at two different study sites in North America. Nestling age, nest code, site code, and brood size were controlled for as random effects in each model. In both models nestling age, nest code, and brood size were significant random effects. ddf = denominator degrees of freedom.

Variable	New York					New Jersey				
	Estimate	SE	ddf	F	P	Estimate	SE	ddf	F	P
Male throat color (PC1)	0.69	1.08	16.4	0.41	0.53	0.50	0.59	57.5	0.69	0.41
Male streamer length (mm)	0.08	0.16	12.7	0.29	0.60	0.04	0.12	36.7	0.11	0.74
Partner feeding	0.47	0.14	37	10.81	0.002	0.30	0.10	90.6	9.59	0.003
Time of observation	−0.16	0.42	32.5	0.15	0.70	<0.001	<0.001	71.6	1.23	0.27

Table 4. No evidence for the good parent hypothesis, differential allocation or reproductive compensation hypothesis as a function of female morphology. Male and female feeding rates (number of feeding visits/hr) as a function of female morphology in New York. Nestling age, nest code, site code, and brood size were controlled for as random effects in each model. In both models, nestling age, nest code, and brood size were significant random effects. ddf =denominator degrees of freedom.

Variable	Female feeding rates					Male feeding rates				
	Estimate	SE	ddf	F	P	Estimate	SE	ddf	F	P
Female belly color (PC1)	0.29	0.68	20.7	0.19	0.67	0.02	0.67	18.8	0.01	0.96
Female streamer length (mm)	0.23	0.27	16.9	0.70	0.41	−0.07	0.22	12	0.12	0.74
Partner feeding	0.48	0.13	30.4	14.71	<0.001	0.36	0.15	32	5.51	0.02
Time of observation	−0.37	0.42	33.7	0.78	0.38	−0.39	0.42	35.7	0.88	0.35

female feeding rates (mean feeding rate ± SD: male = 12.69 ± 5.97, SE = 0.80; female = 11.22 ± 6.27, SE = 0.80; $F_{1, 94} = 1.69$; P = 0.20, nestling age); time of behavior data collection was not a significant variable ($F_{1, 94} = 0.54$; P = 0.47). In New Jersey, we also did not detect significant differences between male and female feeding rates (mean feeding rate ± SD: male = 11.89 ± 6.40, SE = 0.78; female = 12.20 ± 7.84; SE = 0.79; $F_{1, 143} = 0.08$; P = 0.78, brood size); time of behavior data collection was not a significant variable in this model ($F_{1, 143} = 0.18$; P = 0.67).

Discussion

In two populations of North American barn swallows, we did not find evidence that variation in male tail streamer length or ventral color is a predictor of his parental investment (Table 3). Similarly, female tail streamer length or color did not predict her parental effort in New York (Table 4). As such, our results do not provide support for the good parent hypothesis (Table 1; Hoelzer 1989), which predicts a positive association between an individual's phenotype and levels of parental care. In a population of European barn swallows, Perrier et al. (2002) also did not find a relationship between male structural coloration and his feeding rates. However, considering that Perrier et al. (2002) found that coloration is not associated with body condition or overall measures of reproductive success, it is not surprising that this trait did not predict parental care. In other European studies that analyzed relationships between parental investment and tail length (a trait under current sexual selection in this population of barn swallows), there was overall no support for the good parent model (Møller 1988, 1989, 1990).

Burley's (1986) differential allocation hypothesis (Table 1) proposes that individuals choose more attractive mates in order to acquire indirect benefits (e.g. good genes) and will

consequentially provide more parental care so these attractive mates will not break the pair bond. In some cases, differential care of offspring as a function of mate attractiveness has resulted in or allowed for reduced care by the other parent (Burley 1986, Sanz 2001). Our data support the most general differential allocation model because females provided more parental care to shared offspring when paired to darker males in New York and New Jersey (Table 5; Fig. 1a, b) but not when paired to mates of longer streamer length (Table 5; Fig. 2a, b). As such, our data do not support the reproductive compensation model because females did not invest more in the offspring of lower quality (lighter-colored) males. That females differentially allocated investment as a function of male color and not streamer length is not surprising given previous evidence that coloration is a more important signal of quality in North American populations of barn swallows (Safran and McGraw 2004, Safran et al. 2005, Neuman et al. 2007) and suggests that females were investing more in the fitness and reproductive success of their broods when paired to these attractive individuals (Burley 1986). Future studies should thus determine which benefits females receive from darker males if not direct provisioning rates to shared offspring (Table 3).

One interpretation of the differential allocation model predicts that males will decrease their parental effort according to their attractiveness (Burley 1986, Sanz 2001). We did not find support for this prediction because males did not adjust their feeding rate according to coloration in New York or New Jersey (Table 3). Interestingly, reduced care by attractive mates was found in other populations of barn swallows where males with long tail streamers fed relatively lower amounts to shared offspring than their social mates (e.g. Møller 1992b, 1994b, de Lope and Møller 1993; but see Møller 1988, 1989, 1990, Cuervo and Møller 2006). However, considering the evidence that European males with experimentally elongated tails are

Table 5. Evidence for differential allocation to offspring by females paired with dark males. Mixed models of female feeding rates (number of feeding visits/hr) in relation to male sexually dimorphic traits, partner feeding rates, and time in which data was collected at two different study sites in North America. Nestling age, nest code, site code, and brood size were controlled for as random effects in each model. In both models, nestling age, nest, and brood size were significant random effects. ddf =denominator degrees of freedom. The negative relationship between throat color and feeding rates indicate that females paired to darker males fed shared offspring at greater rates (see Fig. 1a, b).

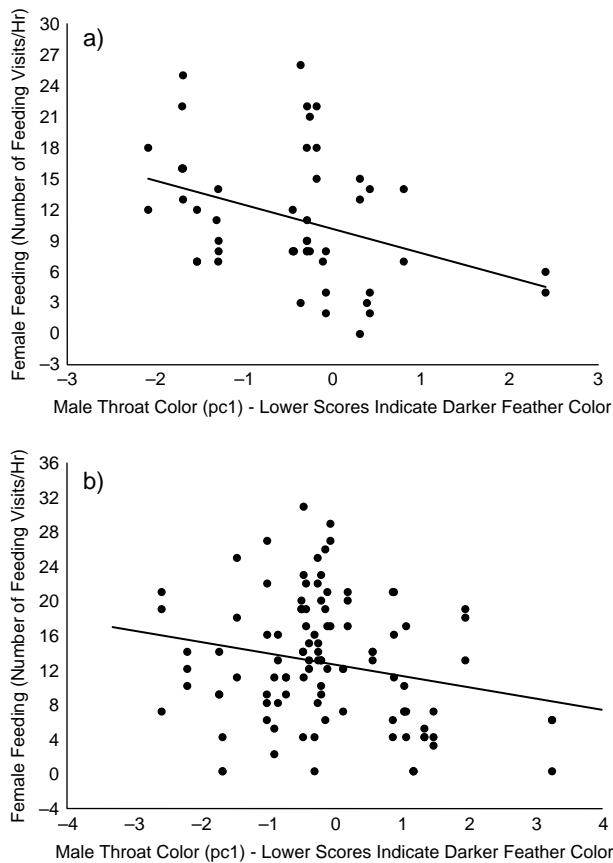| Variable	New York					New Jersey				
	Estimate	SE	ddf	F	P	Estimate	SE	ddf	F	P
Male throat color (PC1)	−2.24	0.89	15.7	6.31	0.02	−1.17	0.60	85	6.65	0.05
Male streamer length (mm)	−0.09	0.14	9.75	0.47	0.51	0.17	0.12	45.2	1.08	0.17
Partner feeding	0.47	0.14	30.4	13.00	0.001	0.36	0.09	91.6	9.59	<0.001
Time of observation	−0.34	0.42	32.5	0.74	0.40	<0.001	<0.001	73.9	1.35	0.25

Figure 1. a) Females fed more when paired to darker males in New York and b) New Jersey. Note that for color axes, lower values indicate darker color. Each observation represents a feeding bout.
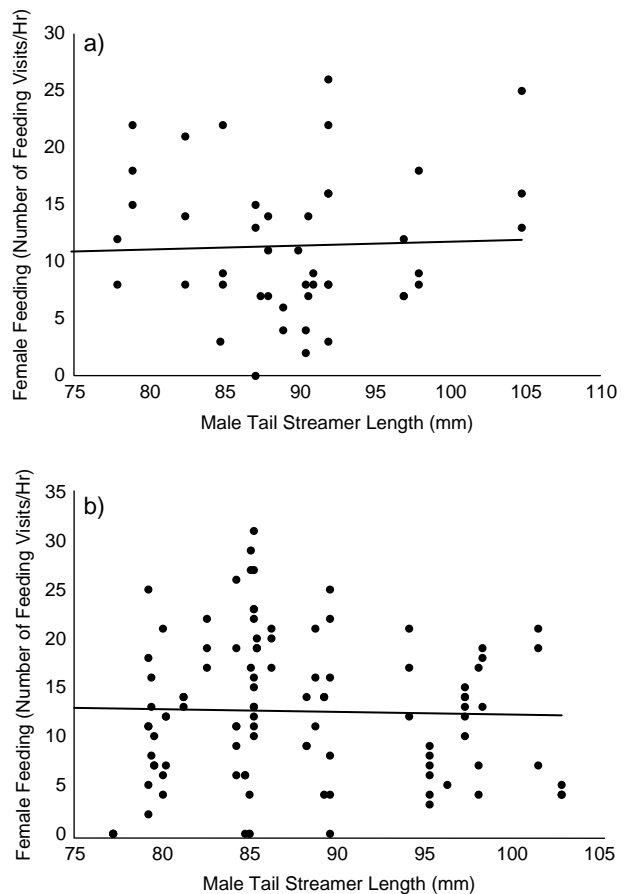

Figure 2. a) Females in New York and b) New Jersey did not increase parental care according to their social mates' tail streamer length. Each observation represents a feeding bout.

impaired in terms of their foraging ability (Møller 1989), Witte (1995) argues that these males reduced their feeding rates because of inefficient aerodynamics rather than quality, *per se*. One possibility for why darker males in our study populations do not decrease parental care is that such a strategy is not adaptive, especially if a reduction in parental care could lead to a net loss in reproductive success. Since ventral plumage coloration is directly related to paternity in North American populations (Safran et al. 2005), it might be detrimental for an attractive male to risk the fitness of his highly related brood in pursuit of mating activities that are costly and time consuming (Clutton-Brock 1991). Alternatively, it is possible that darker individuals do not spend less time feeding nestlings either because the window of opportunity for extra-pair matings is closed or because these dark males more easily acquire extra-pair mates than their lighter neighbors and thus can simultaneously conduct parental care and alternative mating behaviors.

We did not find any association between paternity and parental feeding in either sex (Fig. 3a, b). Considering the costs of time and energy associated with parental investment (Clutton-Brock 1991), it is interesting that males did not make adjustments when their paternity within a brood is mixed. One possibility is that male barn swallows do not have direct or indirect cues by which to assess paternity (Kempenaers and Sheldon 1996) and so do not adjust their

investment to mixed broods. Other experimental studies in non-bird species have avoided this problem because of the adaptations these organisms have in gaining information about paternity (Neff and Gross 2001, Hunt and Simmons 2002, Buchan et al. 2003, Neff 2003, Rios-Cardenas and Webster 2005). Alternatively, even if male swallows are aware of their parentage, it is still not clear whether they would make any adjustments. For example, Davies et al. (1992) suggest that males provide the same level of care even with reduced parentage. This is because total brood fitness — including the fitness of the male's true off-spring — would be lowered if they did not provide care, especially if females did not compensate for a partner that feeds at a lower rate.

Our results also suggest that individuals were influenced by their partners' level of care because we detected a positive correlation between male and female feeding rates (Table 3, 4 and 5; Fig. 4a, b). It is difficult within the context of this study to determine the mechanism behind this observed co-variation because we did not conduct experimental manipulations to explicitly test how pair-mates respond to their partners' parental efforts. However, we did detect a consistent pattern of association in parental care in both study sites because the coefficient estimate for the relationship between male and female feeding rates was positive and less than one, suggesting that females increased their feeding rates to a greater degree than their
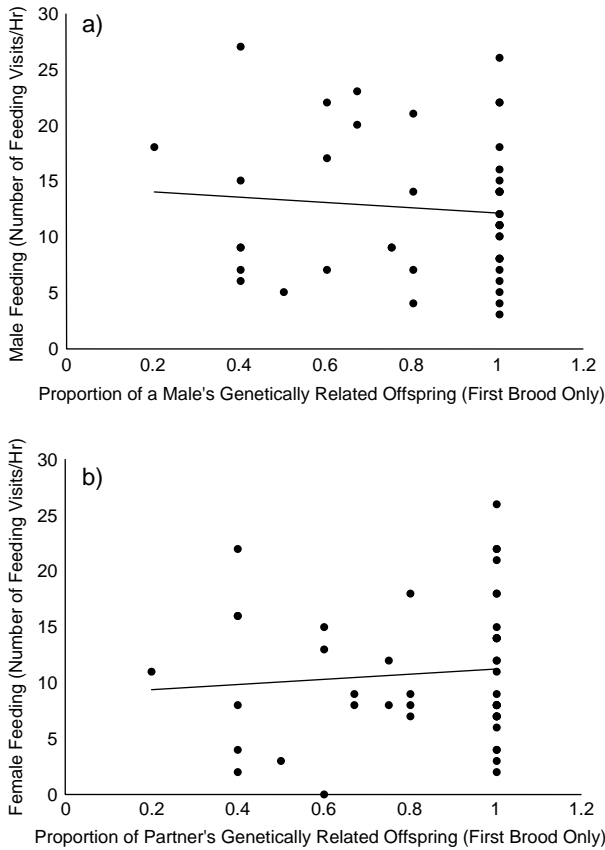
Figure 3. In a New York population of barn swallows, paternity did not influence a) male or b) female feeding rates. Each observation represents a feeding bout.
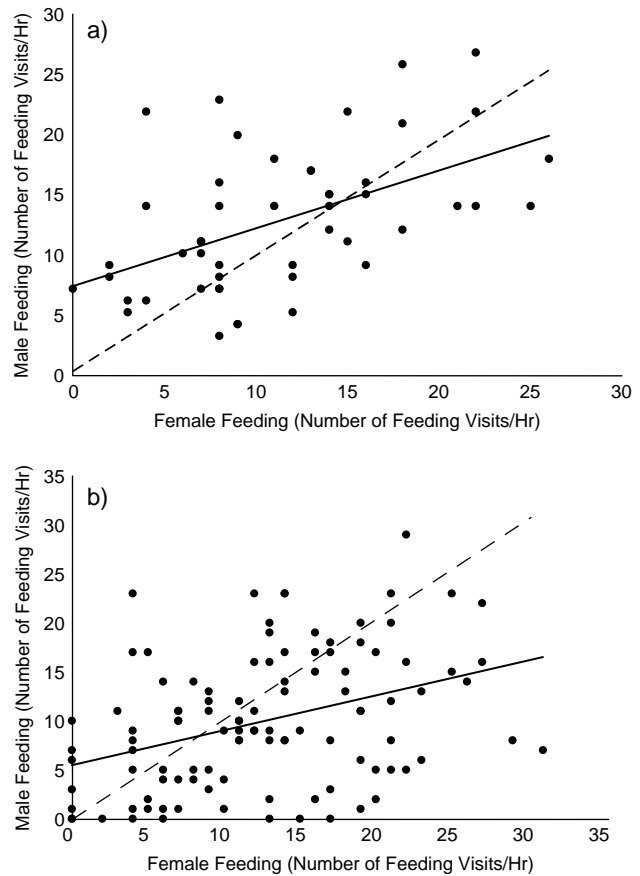

Figure 4. a) Male and female feeding rates were positively correlated in New York and b) New Jersey. Dashed line indicates a 1:1 correspondence in feeding rates for comparison with our data. Each observation represents a feeding bout.

partners' even though male and female feeding rates did not differ throughout the breeding season. In one theoretical model of biparental care, Johnstone and Hinde (2006) propose that males and females will both "match" (with a less pronounced change in the same direction) their partners' change in investment when each parent has partial information regarding brood need (e.g. long-term need) or quality of young (e.g. genetic quality inherited by the partner) and when the variation in brood need is large compared to the variation in parental state. Considering that we found evidence of a matching response to an increase in female care by the male partner, though not to the same extent, future studies should confirm that barn swallows are meeting the criteria underlying Johnstone and Hinde (2006)'s model of biparental care.

A potential limitation of our study is that we only measured feeding rates; it is possible that other indicators of parental care, including food quality would provide additional information. While we found that plumage color does not provide information about feeding rates *per se,* other variables related to parental care may still be related to male color. For example, females may be using color as a cue of mate parental quality if plumage coloration signals ability in providing micronutrients to shared offspring. There is evidence that melanin based plumage coloration, like that found in barn swallows (McGraw et al. 2004, 2005) is conditionally dependent on calcium (Veiga and Puerta 1996, Griffith 2000, Parker et al. 2003), whereby

darker individuals have access to calcium rich resources. Calcium is important for nestling growth and hatching success (e.g. Rosin 2007) and so it would be beneficial for partners to pay attention to these signals during mate selection. Considering this, it has yet to be determined the extent to which micronutrients affects melanin expression. While there is substantial evidence that dietary mineral content affect the expression of melanin, it is by no means the sole factor: hormonal (McGraw 2006), genetic (Mundy 2006), and social (Tibbetts and Dale 2004) processes also shape melanin expression in animals and so future studies should determine the extent to which micronutrients affect melanin expression in barn swallows.

Should male signals reveal their provisioning abilities? Møller and Jennions (2001) found male sexually dimorphic traits are generally not a useful measure of parental feeding, although modeling evolutionary patterns of parental care signals have reached conflicting conclusions (Price et al. 1993, Fitzpatrick et al. 1995, Kokko 1998). Overall, our findings suggest that color and streamer lengths are likely not sexually-selected as signals of parental care, at least in terms of provisioning rates. Instead, our data are most consistent with the idea that females are using male color as a signal of other benefits they can expect to receive and further support the mounting evidence that coloration is a more important signal of quality than tail streamer length in North American populations of barn swallows (Safran and

McGraw 2004, Safran et al. 2005, Neuman et al. 2007, Safran et al. 2008).

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