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MALE EUROPEAN STARLINGS DO NOT USE EGG SPOTS AS A CUE TO ADJUST INVESTMENT IN NESTLINGS

MARK A. W. HORNSBY,^{1,3} EVAN R. FAIRN,^{1,2} AND COLLEEN A. BARBER^{1,4}

ABSTRACT.—The effects of post-laying egg spottiness on nestling condition and parental provisioning were investigated in a nest box-breeding population of European Starlings (*Sturnus vulgaris*). Our objectives were to ascertain whether egg spottiness was associated with the nest ectoparasite *Carnus hemapterus*, and to examine potential relationships between egg spottiness, presence of *C. hemapterus*, nestling condition, and parental provisioning effort in European Starlings. Spotted-egg clutches were present over all 3 years in our population, but the spots did not reflect *C. hemapterus* abundance. Nestlings from spotted-egg clutches did not have more *C. hemapterus* than those from unspotted-egg clutches. However, nestlings from spotted clutches were in better condition than those from unspotted clutches. Nestling condition was not associated with *C. hemapterus* abundance. Adult male and female provisioning rates to the offspring did not differ between spotted and unspotted clutches. Similarly, the proportion of provisioning visits by males did not differ significantly between spotted and unspotted clutches, indicating that parents in our population of European Starlings do not use egg spots as a cue to altering their provisioning effort. Further research is required to fully understand the cause and consequences of egg spots in European Starlings. Received 29 September 2011. Accepted 25 September 2012.

Key words: *Carnus hemapterus*, ectoparasite, egg spots, nestling condition, parental care.

Studies of avian nest ectoparasitism typically focus on the effects parasites have on nestlings (e.g., Fauth et al. 1991, Møller 1991, Merino and Potti 1995, Gwinner et al. 2000) or they examine host-parasite co-evolution (e.g., Martin et al. 2001; Roulin et al. 2001, 2003; Valera et al. 2004; Soler et al. 2005). Recent studies have examined whether parents alter their behavior according to the ectoparasite load of their offspring. The parental food compensation hypothesis (Tripet and Richner 1997; see also Bouslama et al. 2002) proposes that parents will devote more time and energy in provisioning offspring from parasitized broods with high quality food to compensate for costs such as nutrient deficiency and water loss from hematophagous ectoparasites. However, life history theory predicts that parental investment in offspring may vary depending on the perceived reproductive value of the young, which might be evaluated through their parasite load (e.g., Avilés et al. 2009).

Eggs are solid-colored when laid in some species, but develop reddish-brown spots during incubation (e.g., Avilés et al. 2009). These spots are often attributed to ectoparasites (either fecal material or blood from ectoparasites that are

feeding on incubating parents) (Feare 1984, López-Rull et al. 2007, Avilés et al. 2009). Experimental work on the Spotless Starling (*Sturnus unicolor*) has demonstrated that egg spots are associated with the presence of the ectoparasitic fly *Carnus hemapterus* (Diptera: Carnidae) (López-Rull et al. 2007). Further, Avilés and others (2009) found *C. hemapterus* parasitism of Spotless Starlings was negatively associated with nestling condition (mass), and that males provisioned nestlings from spotted-egg clutches less than males from whose clutches the spots had been experimentally removed. They concluded males may be using the spots as an indicator of offspring fitness, perhaps allocating their energy into other efforts (e.g., obtaining new mates) instead of increasing provisioning effort to compensate for the ectoparasitism.

Reddish-brown spots also appear on eggs of European Starlings (*S. vulgaris*) during incubation, and have been previously described (Jackson 1970, Feare and Constantine 1980). European Starlings are also parasitized by *C. hemapterus* (Liker et al. 2001), are socially monogamous with biparental care, yet are facultatively polygynous (Cabe 1993). We investigated whether egg spots of European Starlings were associated with *C. hemapterus*. We also examined whether egg spottiness was correlated with nestling condition and parental provisioning effort to the offspring.

METHODS

Study Site.—A nest box-breeding population of European Starlings was studied on the campus of

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Saint Mary's University in Halifax, Nova Scotia, Canada (44° 39' N, 63° 34' W) from April to July 2010–2012. Forty-five nest boxes were erected at least 2 m above ground on trees in 2007. Old nest material was removed from the nest boxes after each brood had fledged.

Study Species.—European Starlings are secondary cavity-nesters and exhibit biparental care; males and females share incubation and provisioning duties (Ingold 1994, Sandell et al. 1996). Laying occurs in late April and is typically synchronous; females produce 4–6 eggs (Feare 1984). The eggs are a spotless, brilliant pale blue color, possibly evolving in response to predator avoidance or through sexual selection as a signal indicating female quality (Kilner 2006). Eggs are incubated for 12 days (Feare 1984); upon hatching, the nestlings remain in the nest for 21–22 days. Two broods are typically raised each year (Kessel 1953).

C. hemapterus is a small (2 mm) dipteran fly that has been documented in at least 40 avian species from 18 different families (Grimaldi 1997). It tends to favor cavity-nesters and avoid ground-nesting species (Marshall 1981). *C. hemapterus* is considered hematophagous and, upon encountering a suitable host, loses its wings (Marshall 1981, Sivinski 1984, Liker et al. 2001). Maximum *C. hemapterus* intensity on nestling European Starlings occurs 5–7 days post-hatch, when feather development is still minimal yet nestlings are a good size; intensity decreases as the nestlings age, likely because of the ectoparasite's diminished feeding ability when feathers are present (Walter and Hudde 1987, Liker et al. 2001, Hoi et al. 2010).

Field Work.—We documented nesting activity within each nest box in April. When eggs were observed, we noted how many were present and assessed each egg for spottiness (30 nests each in 2010 and 2011, and 27 nests in 2012). We based our methodology of categorizing spottiness of eggs on that of Avilés et al. (2009); however, we grouped clutches into one of two categories: spotted (all eggs had spots) or unspotted (no eggs had spots). Nests in which some eggs were spotted while others were not were excluded from the analysis. Only spotted clutches were present in 2012; we therefore analyzed *C. hemapterus* data from that year but not those for parental provisioning or nestling condition.

Adults were caught with a nest box trap (Stutchbury and Robertson 1986) when nestlings

were 5–6 days of age (day 0 = day of hatch). Adults were classified to sex (Kessel 1951, Feare 1984) and marked with Canadian Wildlife Service (CWS) bands, as well as a unique color band combination for individual recognition.

The number of *C. hemapterus* on nestlings was ascertained when nestlings were 5–6 days of age. Each nestling was removed from the nest and immediately placed in a small white bucket to count the number of *C. hemapterus* present on it. We calculated both total *C. hemapterus*/brood and mean *C. hemapterus* abundance/nestling within a brood (total *C. hemapterus* on all nestlings in the brood/number of nestlings).

Nestling morphometrics were taken on day 5 or 6 (day 5/6) and day 11 or 12 (day 11/12) post-hatch. Mass was taken to the nearest 0.5 g using a Pesola spring balance. Tarsus length was recorded to the nearest 0.01 mm using digital calipers; three to five measurements were made, and mean tarsal length was used in analyses. We used residuals calculated by regressing mass on tarsus length as a measure of nestling condition on each of days 5/6 and 11/12 post-hatch. We calculated one index of condition/brood on each of days 5/6 and 11/12 by averaging the residuals for each nestling in a brood, thereby avoiding pseudoreplication. We calculated one overall index of condition for each brood by averaging the two residuals (days 5–6 and 11–12) for each brood.

Parental provisioning behavior was documented for 1 hr at each nest over two different stages of the nestling period: on days 7/8 and 13/14 post-hatch. Provisioning watches began with the arrival of a parent with food between 0700 and 1100 hrs (AST) when adults are active in provisioning offspring (Tinbergen 1981, Mennechez and Clergeau 2006). Observers sat at least 10 m from the nest to ensure adult behavior was not affected. The sex of the adult was noted with binoculars at each provisioning event, as was the number of times males and females provisioned. Nestlings were counted after each provisioning watch to ascertain brood size. We considered each time an adult entered its nest box to be a provisioning event, which was typically corroborated by the visible presence of food in the adult's beak.

We calculated the mean number of provisionings/nestling to obtain a measure of paternal provisioning effort by summing the number of visits made by males over the day 7/8 and day 13/14 nestling periods and dividing it by brood size (mean number of provisionings/nestling). We

TABLE 1. Medians, ranges, and sample size for the total number of *C. hemapterus*/brood of European Starlings over 3 years (2010, 2011, 2012).

Year	Median			Range		Sample size		
	All	Spotted	Unspotted	Spotted	Unspotted	All	Spotted	Unspotted
2010	1	1	2.5	0–32	0–14	30	11	6
2011	0	0	0	0–5	0	30	11	3
2012	2	2	n.a.	0–37	n.a.	27	27	0

were unable to obtain provisioning data at all spotted- and unspotted-egg nests but were successful for the majority. Maternal provisioning effort was similarly calculated. The proportion of paternal provisioning was estimated by summing the number of male provisions made on days 7/8 and 13/14 of the nestling period and dividing it by the total number of provisionings made by both males and females over these two time periods.

Statistical Analyses.—Data were analyzed using GraphPad Prism 5.03 statistical software (GraphPad Software, San Diego, CA, USA). Nestling condition and parental provisioning effort data were pooled across 2010–2011, because the proportion of spotted to unspotted clutches did not vary significantly between these 2 years. These data were also pooled across early and late broods to gain statistical power, as no significant differences were found between them with respect to proportion of spotted to unspotted clutches. Sample sizes were three spotted, two unspotted clutches (2010 Early); eight spotted, four unspotted (2010 Late); seven spotted, two unspotted (2011 Early); and five spotted, one unspotted (2011 Late) resulting in 23 spotted- and nine unspotted-egg clutches. All data were tested for normality using the D’Agostino and Pearson omnibus normality test, and the appropriate statistical test was performed. Mean \pm SE are given unless otherwise stated. All tests were two-tailed. Results were considered significant when $P \leq 0.05$.

RESULTS

We found 116 *C. hemapterus* on nestlings in 2010 ($n = 30$ nests), but only 11 *C. hemapterus* on nestlings in 2011 ($n = 30$ nests). In 2012, 117 *C. hemapterus* were detected on nestlings ($n = 27$ nests). The total number of *C. hemapterus*/brood differed among years (Kruskal-Wallis $H = 16.99$, $df = 2$, $P < 0.001$; Table 1). There were significantly fewer *C. hemapterus*/brood in 2011 than in 2010 (Dunn’s multiple comparison post-test,

$P < 0.01$) and fewer in 2011 than in 2012 (Dunn’s post-test, $P < 0.001$). There was no significant difference in total *Carnus* number/brood between 2010 and 2012. Similarly, the prevalence of *C. hemapterus* did not differ between 2010 (56.7%) and 2012 (66.7%) (Fisher’s Exact test: $P = 0.59$) but did differ when 2011 data (16.7%) were included ($\chi^2 = 16.41$, $df = 2$, $P < 0.001$).

The total number of *C. hemapterus* on 5/6 day-old nestlings did not differ between spotted- and unspotted-egg clutches in either 2010 (Mann-Whitney $U = 31.00$, $n_1 = 11$, $n_2 = 6$, $P = 0.88$; Table 1) or 2011 (Mann-Whitney $U = 13.5$, $n_1 = 11$, $n_2 = 3$, $P = 0.52$; Table 1). All clutches ($n = 27$ nests) in 2012 contained spotted eggs; no unspotted-egg clutches were present. Some nests with spotted eggs in 2010 (4/11, 36.4%) had no evidence of *C. hemapterus* on the nestlings while 66.7% (4/6) of nests with unspotted eggs had *C. hemapterus* on nestlings. This trend was not observed in 2011 as all *C. hemapterus* were found only on nestlings from spotted-egg clutches, but the sample size of unspotted-egg clutches was small ($n = 3$ nests). In 2012, 33% (9/27) of nests with spotted eggs had no evidence of *C. hemapterus* on nestlings. The proportion of spotted- to unspotted-egg clutches did not differ between the two intensively studied years (65% and 79% of clutches were spotted in each of 2010 and 2011; Fisher’s Exact test: $P = 0.46$) but did differ when 2012 data (100% of clutches were spotted) were included ($\chi^2 = 10.4$, $df = 2$, $P = 0.006$). We pooled the data from 2010–2011 when analyzing nestling condition and parental provisioning effort. Similarly, the proportion of spotted- to unspotted-eggs clutches did not differ between early (71%; 10/14 spotted) and late broods (72%; 13/18 spotted) (Fisher’s Exact test: $P = 1.0$), nor did the mean number of *C. hemapterus* per nestling differ between early and late broods (Mann-Whitney $U = 92.5$, $n_1 = 14$, $n_2 = 18$, $P = 0.17$). There was no difference in median *C. hemapterus*/nestling between spotted- (median = 0, range = 0–6.4) and

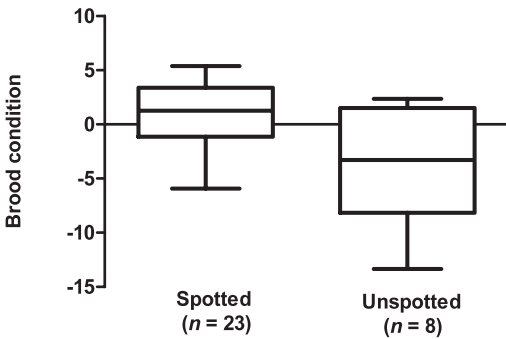


FIG. 1. Median, minimum, and maximum brood condition (residuals) in spotted- and unspotted-egg clutches of European Starlings.

unspotted-egg clutches (median = 0, range = 0–4.7) for 2010 and 2011 (early and late broods) combined (Mann-Whitney $U = 103.5$, $n_1 = 23$, $n_2 = 9$, $P = 0.98$).

Nestlings from spotted-egg clutches were in significantly better condition than those from unspotted-egg clutches (Mann-Whitney $U = 46.00$, $n_1 = 23$, $n_2 = 8$, $P = 0.04$; Fig. 1). Nestling condition, however, was not correlated with the mean number of *C. hemapterus* per nestling ($r_s = 0.0629$, $n = 31$, $P = 0.74$). We found no difference in first-egg dates between spotted- and unspotted-egg clutches (mean Julian date \pm SE = 9.5 ± 1.11 and 9.4 ± 2.02 , respectively; unpaired $t = 0.03554$, $df = 30$, $P = 0.97$). Similarly, clutch size between spotted- and unspotted-egg clutches did not differ (mean \pm SE = 4.8 ± 0.14 and 4.9 ± 0.31 , respectively; unpaired $t = 0.2394$, $df = 29$, $P = 0.81$). There was no difference in nestling survival at 13–14 days of age for nestlings hatching from spotted- and unspotted-egg clutches (mean number of nestlings \pm SE = 3.4 ± 0.29 and 3.0 ± 0.67 , respectively; unpaired $t = 0.7057$, $df = 30$, $P = 0.49$).

Paternal provisioning effort to nestlings (mean number of provisionings/nestling/hr) did not differ between spotted and unspotted clutches (Mann-Whitney $U = 47.5$, $n_1 = 17$, $n_2 = 7$, $P = 0.46$; Fig. 2). Similarly, maternal provisioning effort did not differ between spotted- and unspotted-egg clutches (Mann-Whitney $U = 42.5$, $n_1 = 17$, $n_2 = 7$, $P = 0.29$; Fig. 2). There was no difference in the proportion of male provisionings to offspring from spotted- and unspotted-egg clutches (mean \pm SE = 0.41 ± 0.06 vs. 0.30 ± 0.08 ; unpaired $t = 1.052$, $df = 22$, $P = 0.30$).

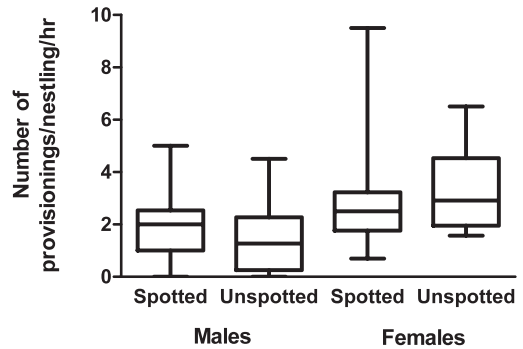


FIG. 2. Median, minimum, and maximum number of feeding visits by adult male and female European Starlings to nestlings hatched from spotted- ($n = 17$) and unspotted-egg ($n = 7$) clutches.

DISCUSSION

The presence of spots on European Starling eggs in our study population does not appear to be related to the presence or number of *C. hemapterus*. Our findings are counter to those of López-Rull and others (2007) who reported egg spots were indicative of *C. hemapterus* abundance in Spotless Starling nests; they found a positive relationship between *C. hemapterus* abundance and egg spots. We observed no *C. hemapterus* in several spotted-egg nests (in 2010 and 2012), and detected *C. hemapterus* in unspotted-egg nests. Adult *C. hemapterus* live for 2 days, and have not been reported to feed on adult avian hosts (Valera et al. 2004; but see Feare 1984). Their short life span may explain why we did not detect them in some spotted clutches. Our findings indicate *C. hemapterus* are not the source of egg spots in our study population. We detected other hematophagous ectoparasites, such as lice, fleas, and mites (T. D. Galloway, pers. comm.) in nests, lending support to their potential role in causing the spots.

The numbers of *C. hemapterus* counted in this study (116 on nestlings from 30 nests in 2010, 11 on nestlings from 30 nests in 2011, and 117 on nestlings from 27 nests in 2012) were low compared to results obtained by Liker and others (2001) who found 2,775 *Carnus* spp. in 33 nests of European Starlings in Budapest, Hungary. They calculated the median *C. hemapterus*/brood of 54, while we found medians of one, zero, and two *C. hemapterus*/brood over the 3 years in our breeding population. Liker and others (2001) detected a

median of nine *C. hemapterus*/nestling, while we found a median of no *C. hemapterus*/nestling. Other avian species also had high *C. hemapterus* abundance; Cannings (1986) detected 65 *Carnus* spp. in three nests of Northern Saw-whet Owls (*Aegolius acadicus*), while Dawson and Bortolotti (1997) found 363 *Carnus* spp. in 50 nests of American Kestrels (*Falco sparverius*). Our findings are also low compared to nests of Barn Owls (*Tyto alba*; Roulin et al. 2003), which had a mean of 50 ± 5 *C. hemapterus*/nestling, and those of Spotless Starlings with reports of 16.6 ± 12.6 *C. hemapterus*/nestling (López-Rull et al. 2007). Prevalence of *C. hemapterus* was also lower in our population (57, 67, and 17% in each of the years studied) compared to the 94% prevalence reported by Liker and others (2001) in their European Starling population.

We may have observed a lower abundance and prevalence of *C. hemapterus* than expected in our breeding population, because we removed old nesting material between broods and years. However, studies reporting the highest numbers of *C. hemapterus* (e.g., Dawson and Bortolotti 1997, Liker et al. 2001) also removed old nesting material once breeding was complete. López-Rull and others (2010) detected more *C. hemapterus* in later than in early Spotless Starling broods. We did not detect a difference in *C. hemapterus* abundance between early and late broods, nor did Dawson and Bortolotti (1997) for American Kestrels. Environmental factors likely have a large role in affecting *Carnus hemapterus* abundance in nests. Merino and Potti (1996) found that more rainy and colder weather than usual had a significant role in abundance and prevalence patterns of ectoparasites in the European Pied Flycatcher (*Ficedula hypoleuca*). Heeb and others (2000) found that experimentally decreased humidity significantly increased ectoparasitic infestation in the Great Tit (*Parus major*). Future research should include investigation into how abiotic environmental and ecological factors influence abundance of *C. hemapterus*.

Nestlings from spotted-egg clutches were in better condition than those from unspotted-egg clutches. First-egg date, clutch size, and nestling survival until 13/14 days post hatch did not differ significantly between spotted- and unspotted-egg clutches. Abundance of *C. hemapterus* had no effect on nestling condition. If another species of hematophagous ectoparasite caused the spotting, then perhaps it preferred nestlings that were in

better condition. Dawson and Bortolotti (1997) discovered that heavier male American Kestrel nestlings had a higher *C. hemapterus* load than did lighter nestlings, and that female nestlings with longer tenth primaries tended to have higher *C. hemapterus* abundance than those with shorter tenth primaries. Consistent with our findings, Liker and others (2001) found that nestling growth and mortality rates in European Starlings were unaffected by *C. hemapterus* abundance. Nestling condition and mortality rate were also unaffected by *C. hemapterus* abundance in American Kestrels (Dawson and Bortolotti 1997). However, Avilés and others (2009) reported nestling condition (mass) was negatively correlated with *C. hemapterus* abundance in Spotless Starlings.

Male and female European Starlings did not alter their provisioning to nestlings from spotted-compared to unspotted-egg clutches. Thus, the higher condition of nestlings hatching from spotted-egg clutches than from unspotted-egg clutches is not a result of increased parental provisioning. Our findings do not support those of Avilés and others (2009) who reported male Spotless Starlings provisioned offspring less when egg spots were present, in accordance with life history theory, and not the parental food compensation hypothesis. Our findings do not support either of these hypotheses. Our results may be best explained by possible differences among ectoparasites feeding on nestlings, and their community structure within the starling nests. There were many hematophagous ectoparasites in our nests. Perhaps unspotted-egg clutches were more heavily infested with ectoparasites feeding on nestlings compared to spotted-egg clutches. Alternatively, the spatial distribution of spotted- and unspotted-egg clutches within our field site may have led to unequal environmental and abiotic conditions, possibly leading to higher ectoparasitic infestation in some areas but not others. However, our field site is not large; thus, even if spotted- and unspotted-egg clutches were as spatially separated as possible, environmental variables were not likely to differ. Other well-known drivers of ectoparasitic prevalence patterns, including host species density in bats (Czenze and Broders 2011) and molting stage in birds (Hamstra and Badyaev 2009) are also not likely to have had a role in our population. However, there is some evidence that European Starlings selectively choose 'fumigating' materials with which to build a nest

(reviewed in Clayton et al. 2010). It may be that adults whose nestlings were in worse condition (unspotted-egg nests) did not use as many or enough high-quality fumigating nesting material as adults whose nestlings were in better condition (spotted-egg nests). Our *a priori* objective was to investigate *C. hemapterus* ectoparasitism and its associated effects as indicated by our methodology. We suggest future investigations attempt a comprehensive nest and ectoparasite examination, instead of focusing solely on *C. hemapterus*.

Our study provides no evidence that *C. hemapterus* causes egg spots in European Starlings, nor does it suggest that parents use egg spots to make decisions on provisioning behavior. *C. hemapterus* did not appear to have any negative effects on nestlings as nestling condition and survival to 13/14 days of age were unaffected by the number of *C. hemapterus* on nestlings. However, nestlings from spotted-egg clutches were in better condition than those from unspotted-egg clutches. Future research should investigate the role of other ectoparasites in nests of European Starlings to identify which may cause egg spots.

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