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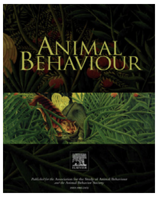

Adjustment of total activity as a response to handicapping European starlings during parental care

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Parental care is widely assumed to be costly, and life-history theory predicts that individuals that invest more in parental care should benefit in terms of number of offspring produced but that increased parental care might come at a cost in terms of decreased future fecundity and/or survival. However, the notion that parents that work ‘harder’, commonly measured by the rate at which parents visit the nestbox to provision their chicks, produce more, fitter chicks is surprisingly poorly supported. One potential reason for this apparent lack of relationship between measured workload during parental care and breeding productivity is that nest visit rate does not provide a good measure of foraging effort. Here, we used an automated radiotelemetry system to measure activity of individual female European starlings, *Sturnus vulgaris*, during breeding, combined with a handicapping experiment (combination of radiotransmitters and wing clipping) and measures of foraging metrics, current breeding productivity, future fecundity and return rate. Handicapping decreased current breeding success due to higher abandonment and nest failure, but among successful birds (fledging ≥ 1 chick) there was no effect of handicapping on brood size at fledging for the current breeding attempt. Handicapping decreased future fecundity, the probability of initiating a second brood, and return rate, but there was no evidence for additive costs of reproduction in wing-clipped females. Handicapping had no effect on provisioning rate but automated tracking data showed that, during chick rearing, wing-clipped females had 22% lower activity compared to females with radios only. Our data provide an explanation for the often contradictory effects of handicapping reported on reproductive effort and costs of reproduction: individuals can use behavioural flexibility – decreasing overall activity while maintaining provisioning rate – along with changes in mass and nestling diet to mitigate putative effects of increased workload imposed by handicapping.

The trade-off between survival and reproduction is central to life-history theory: individuals must balance resource allocation towards current reproductive effort, future reproduction and survival (Stearns, 1992). Individuals that invest more resources into current reproduction should benefit by raising more and better-quality offspring, but those same individuals might pay a cost of increased parental effort in terms of reduced future fecundity and/or survival (Clutton-Brock, 1991; Royle, Smiseth, & Kolliker, 2012). Despite the centrality of these ideas for life-history theory, unequivocal evidence to support this trade-off is surprisingly weak, particularly in females (Santos & Nakagawa, 2012). In birds, a common approach to test ideas about costs of reproduction involves ‘handicapping’ individuals, either by addition of weights (e.g. radiotransmitters) or through decreasing wing area (e.g. wing clipping). In theory, these experimental manipulations cause a direct, inescapable biomechanical effect through increased wing loading, making birds work harder or incur higher flight costs during central place foraging associated with parental care. Therefore, if parents choose to maintain their provisioning effort, this must come as a physiological or energetic cost. Parents should then adjust their investment in offspring care, e.g. they might decrease investment in current offspring (decreasing provisioning rate) and maintain investment in self-maintenance (e.g. foraging and immune function), or they might maintain investment in the current breeding attempt but pay a greater ‘cost of reproduction’ (decreased future fecundity and/or survival).

Handicapping studies during parental care in birds have produced mixed results in relation to costs of reproduction. Numerous studies using small tracking devices (<5% body mass) have reported

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no change in provisioning rate or the number of chicks fledged (productivity) (Barron et al., 2010, 2013; Fowler & Williams, 2017; Neudorf & Pitcher, 1997; Rivers, Newberry, Schwarz, & Ardia, 2017). Some studies utilizing wing clipping found that clipped birds reduce their provisioning rate to chicks and have lower productivity (Jacobs, Elliott, & Gaston, 2013; Slagsvold & Lifjeld, 1988), but do not have different return rates (local survival in subsequent years) than nonmanipulated birds (Bijleveld & Mullers, 2009; Wright & Cuthill, 1989). However, in other studies, even though wing-clipped birds reduced provisioning rates, they had lower return rates with either no difference in productivity (Winkler & Allen, 1995) or even a decrease in current productivity (Love & Williams, 2008). There are a number of possible reasons for these contradictory results, which we explore in this paper. First, costs of reproduction might not be expressed in the current (manipulated) breeding attempt but can be deferred to subsequent life stages, so it is critical to evaluate future fecundity and survival (Williams, 2012). Second, responses to either natural or experimentally induced variation in brood demand or parental effort could be dependent on ecological context (Hegemann, Matson, Flinks, & Tieleman, 2013; Mathot et al., 2017; Williams, 2018), e.g. annual differences in food availability, requiring studies over multiple years. Third, the most commonly used measure of parental investment is provisioning rate, or nest visit rate, which might not provide a good measure of parental ‘workload’. Evidence that increased provisioning rate leads to more or better-quality chicks is equivocal (Fowler & Williams, 2015; Moreno, Cowie, Sanz, & Williams, 1995; Schwagmeyer & Mock, 2008) especially as there is marked (5–10 fold) individual variation in provisioning rate in chick-rearing birds (Williams, 2012). Individual birds might alter their foraging behaviour during chick rearing in other ways, e.g. varying load size, prey type, foraging distance or other components of overall activity (Mariette et al., 2011; Stauss, Burkhardt, & Tomiuk, 2005; Weimerskirch, Chastel, & Ackermann, 1995; Wright, Both, Cotton, & Bryant, 1998).

Most studies of parental workload have focused on activities at the nest (i.e. nest visit rate provisioning behaviour) (but see Mariette et al., 2011; Stauss et al., 2005). However, recent technological developments now allow researchers to monitor individual free-living animals 24/7 (Wilmers et al., 2015). Automated radiotelemetry allows for the collection of daily activity data of individuals during the breeding season over an extended period and has been used to quantify nocturnal extraterritorial forays (Ward, Alessi, Benson, & Chiavacci, 2014), fever and sickness behaviour in sparrows (Adelman, Córdoba-Córdoba, Spoelstra, Wikelski, & Hau, 2010) and activity rhythms under constant daylight in the Arctic (Steiger et al., 2013). However, this technology has yet to be used to quantify parental activity, or workload, in chick-rearing birds in relation to breeding productivity. Also, most studies quantifying parental activity restrict their analysis to a short window, typically 30 min observations over the course of a couple of days during the chick-rearing period (García-Navas & Sanz, 2011; Mariette et al., 2011; Schwagmeyer & Mock, 2008; Stauss et al., 2005). Automated radiotelemetry can monitor individual activity during parental care remotely throughout the entire breeding period.

Here, we used an automated radiotelemetry system to constantly monitor the diurnal activity of individual female European starlings, *Sturnus vulgaris*, from late incubation through the entire chick-rearing period, in two different years. We combined radiotracking with video analysis of prey brought back to the nest and a handicapping experiment (radiotransmitter attachment, wing clipping and a control without a radiotransmitter attachment) to investigate changes in overall activity in response to experimentally increased workload and to obtain measures of current breeding productivity (e.g. number and size of fledglings), future fecundity (e.g. productivity of second broods and productivity in the subsequent year) and survival (local return rate) for all females in relation to treatment. We predicted that handicapped individuals would maintain investment in the current brood but at a cost in terms of decreased future fecundity and/or survival, and that this cost would be higher in wing-clipped birds than in radio-only birds (due to an incremental effect of handicapping) unless handicapped individuals modulate any cost of reproduction by changing overall activity (independent of provisioning rate) or some other component of foraging (e.g. load size, prey type).

METHODS

Breeding Data

We collected breeding data on European starlings from March through June in 2015 and 2017 from our long-term, nestbox breeding study population at Davistead Farm, Langley, British Columbia, Canada (49°10′N, 122°50′W). Each year, we followed the same basic field protocol: nestboxes were checked daily from late March to determine laying date, individual egg size and clutch size. Nests were monitored until either failure or fledging to quantify productivity. Each nest was checked on day 17 (shortly prior to fledging) to obtain brood size at fledging, fledgling mass, tarsus and wing chord. At the nestbox, all individual breeding females (including the control group) were captured in their nestbox during mid-incubation by plugging the nestbox before dawn, measured (mass, tarsus, wing chord) and fitted with colour leg bands and individually numbered metal bands (Environment Canada permit number 10646). In 2016 only, 29 females were recaptured during days 10–12 of chick rearing and body mass was recorded. Breeding data were collected for individuals, which double-brooded in the same year, as a measure of future fecundity. In subsequent years we relocated all banded females to obtain data on return rate (local survival) and breeding productivity for first and second broods in the year after experimental manipulation (future fecundity). Each female was assigned to one of three treatment groups: nonmanipulated control females (ctrl), females with radiotransmitters (RT) and wing-clipped females with radiotransmitters (clipRT) (Table 1). Females were assigned to treatments sequentially to control for laying date and ‘quality’ (see below). Males were not captured or banded, and thus their identity was unknown, but we obtained nestling diet and provisioning data (see Provisioning Data below) for focal males visiting specific nestboxes.

Provisioning Data

Parental provisioning rate was determined via observations conducted from 0900 hours to 1400 hours on days 6–8 and days

Table 1
Total sample sizes and nest fate for 2015 and 2016 combined, by treatment and subsequent nest fate

Treatment	Year	Initial *N*	Nest fate			
			Abandoned	Failed	Successful	% Success
Control	2015	20	0 (0)	1 (0)	19	95.0
RT	2015	15	1 (0)	2 (0)	12	80.0
clipRT	2015	15	6 (0)	2 (1)	7	46.7
Control	2016	23	1 (0)	2 (0)	20	87.0
RT	2016	22	1 (1)	9 (2)	12	54.5
clipRT	2016	21	7 (1)	5 (4)	9	42.9

RT = radiotransmitter only; clipRT = radio + wing clipping. Numbers in parentheses refer to abandoned/failed birds that laid replacement clutches. See Methods for definitions.

12–14 posthatching for 30 min (day 0 was defined as the day the majority of chicks in the nest hatched). The timing of observations was standardized (see Fowler & Williams, 2015, for more details).

In addition, we recorded the number and type of prey delivered by each parent to nests of radiotransmitter birds using video cameras (Canon VIXIA HF R52), placed approximately 5 m from each nestbox, on days 6–8 and 12–14 posthatching for at least 35 min. Videos were analysed using VLC Media Player. Only 30 min of the video were analysed and the first 5 min were used as a buffer between disturbances at the nest.

Wing Clipping

Adult females were caught during mid-incubation and alternately assigned to either the control, clipRT or RT treatment (with the exception that clipRT females from 2015 who returned in 2016 were automatically assigned as controls in 2016 and removed from control group analyses, $N = 4$). There was no difference in laying date ($t_{71} = 0.87$, $P = 0.39$), clutch size ($t_{71} = -1.36$, $P = 0.18$) or body mass at incubation ($t_{71} = 0.23$, $P = 0.81$) for females subsequently assigned to each treatment. Birds assigned to the clipRT treatment had every third primary feather (i.e. primaries 2, 5, 8) removed from each wing near its base with scissors.

Automated Radiotelemetry

In 2015 ($N = 30$) and 2016 ($N = 42$) females were fitted with a digitally coded Nanotag radiotransmitter (NTQB-4-2, Lotek Wireless Inc., Newmarket, Ontario, Canada) by means of a leg loop harness (Rappole & Tipton, 1991). For the duration of the breeding season, we erected five (2015) or four (2016) Automated Receiving Units (ARUs; Lotek Wireless Inc.) with two to four five-element Yagi antennas around the field site to allow for continuous reception of radio signals from tagged individuals. The receivers were placed strategically throughout the study site to capture all of the nestboxes and potential foraging areas (based on preliminary handheld tracking in 2013–2014; Fowler, n.d.). Every 8 s, each antenna at each tower alternately scanned for deployed radiotransmitters, allowing continuous monitoring of all tagged females' activity. Preliminary validation confirmed that tags were detected up to distances of approximately 1 km.

We calculated ‘activity’ of females during chick rearing following methods described in Steiger et al. (2013), Ward et al. (2014) and Zúñiga et al. (2016). In our activity analysis, we used data from a single ARU and the antenna that was closest to the focal nestbox, i.e. with the strongest average signal for a given individual in our activity analysis (preliminary analysis showed that using data from an adjacent antenna for the same ARU gave quantitatively similar results for activity estimates). Lotek receivers use power as a received signal strength indicator (RSSI) (1 RSSI value, or power, is approximately 2.2 dBm (1.66 mW); Lotek Wireless Inc., personal communication). We applied a minimum threshold power of 50 to control for background noise, which, when converted to signal strength, is consistent with previous studies (references above). We tested whether estimated activity was dependent on choice of specific threshold values, but activity using power thresholds of 30 and 10 were highly correlated with using a threshold power of 50.

The power of an inactive bird is relatively constant from one detection to the next, resulting in a relatively low variance in power, whereas power varies greatly from one detection to the next when an active bird moves relative to a stationary antenna (Greives et al., 2015; Ward et al., 2014). We used the change (Δ) in power from one detection to the next to determine whether a bird was active or inactive. We determined threshold values for Δ power by observing the Δ power of observed incubating, or inactive, females. A Δ power value ≤ 10 indicates an inactive bird. This value is equal to the upper end of the 99% confidence interval of the mean for observed incubating birds (a threshold Δ power of 10 or 5 gave quantitatively similar results). A Δ power threshold of 10 when converted to signal strength (4.5 dBm) is similar to values used in previous studies as thresholds for ‘activity’ (Adelman et al., 2010; Steiger et al., 2013; Ward et al., 2014). An individual's diurnal activity was calculated by dividing the number of ‘active’ detections (Δ power ≥ 10) as a percentage of all detections, and we restricted activity analysis to daylight hours using time of civil twilight (National Research Council Canada, http://www.nrc-cnrc.gc.ca/eng/services/sunrise/).

Statistical Analysis

Statistical analyses were completed in R Studio v.0.98.1028 (R Studio, Boston, MA, U.S.A.) or SAS v.9.4 (SAS Institute, Cary, NC, U.S.A.). Frequency data on nestling diet composition were analysed using chi-square (proc FREQ). We used linear mixed-effects models (proc MIXED) to compare variation in breeding productivity, chick size and mass and foraging metrics with treatment and year as main effects. Among our total records ($N = 116$) we had nine females sampled in both years (18/116, or 16%), representing a moderate level of ‘pseudoreplication’. We therefore included female identity (‘female ID’) as a random effect in these models, which decreased reported degrees of freedom (excluding ‘female ID’ increased degrees of freedom but did not affect the main results reported for any main effect or interaction in any of the analyses). For metrics of future reproduction, we first tested for year effects (nonsignificant in all cases; see Results), then ran models with year as a random factor (models without a year term gave the same results). We categorized individuals based on the fate of their nest (abandoned, failed or successful). Bird classified as abandoned, abandoned their nests immediately following the experimental manipulation. Birds classified as failed continued to incubate and hatch their eggs following the treatment, but the chicks ultimately did not survive and fledge. Bird classified as successful, successfully fledged chicks. For analysis of activity data we included year, year $*$ treatment and either breeding stage and day as main effects (depending on the specific analysis), and number of detections as a covariate. For binary data (initiating second brood, return rate), we used logistic regression (proc LOGISTIC). We then generated lsmeans activity for each individual from these models (for days 6–21 of chick rearing only, i.e. excluding brooding for days 0–5) and compared individual variation in activity to measures of current productivity, future fecundity and return rate with treatment as a main effect and year as a random factor (because of technical failure of radiotags in 2015, where birds broke off the antennas, samples sizes were quite small especially for clipRT females: $N = 4$ in 2015).

Ethical Note

The Canadian Committee on Animal Care (CCAC) approved the research methods described in this paper under Simon Fraser University's Animal Care Committee permit number 1018 B-96. The banding permit to capture and band birds was granted by Environment Canada under permit number 10646 (T.D.W., master permittee) and 10646 N (subpermit to M.W.S.). To reduce the overall stress on the experimental birds, we attempted to reduce the handling time of both the RT and the clipRT birds. Average handling time for both treatment groups was 6.5 min, and there was no statistical difference in the handling time between treatment groups ($t_{49} = 0.63$, $P = 0.53$). The weights of the transmitters were between 1.9 g and 2.1 g or about 2.5% of mean body mass of females at incubation (82.9 g). This is well below the recommended weight of radiotransmitters considering the individual's mass (Barron et al., 2010). In addition, recaptured females did not have their radiotransmitters from the previous year, suggesting that most transmitters fell off following the breeding period. A few females ($N = 5$) still had their radiotags from the previous year. These birds showed no sign of feather wear or skin damage and radios were removed at mid-incubation, so no birds retained a radiotransmitter through their second chick-rearing period.

RESULTS

There was a significant effect of treatment (control, RT, clipRT) on nest fate of first breeding attempts (Table 1). Immediate nest abandonment (before hatching) occurred more frequently for clipRT females (36.1%) than for RT (5.4%) and control (2.3%) females. Overall nest success (fledging > 0 chicks) was highest in control nests (90.7%), lowest in clipRT nests (44.4%) and intermediate in RT nests (64.9%; $\chi^2_2 = 19.56$, $P < 0.001$; Table 1). Of 37 females whose nests failed or were abandoned, nine (24.3%) laid replacement clutches, seven of which were successful. These replacement breeding attempts were included in subsequent analysis of total annual and 2-year productivity (see below), but not in the analysis of the first (current) breeding attempt.

Effects of Manipulation on Current (First) Breeding Attempt

For successful females (i.e. those that fledged at least one chick), there was no effect of treatment, year or treatment∗year on brood size at fledging for first broods ($P > 0.13$ in all cases; Fig. 1a). Including birds that hatched chicks but failed before fledging, there was a treatment effect on the number of chicks fledged ($F_{2,11} = 4.67$, $P = 0.034$; no treatment∗year interaction: $P = 0.74$; Fig. 1a). On average, control birds fledged 4.0 chicks, while RT birds and clipRT birds fledged 2.7 and 2.6 chicks, respectively. RT and clipRT females had similar brood size at fledging ($P > 0.70$), but both treatment groups fledged fewer chicks than control females ($P \leq 0.05$ in both cases; Fig. 1a). In this model there was also a main effect of year ($F_{1,11} = 6.57$, $P = 0.026$): with average fledging success being higher in 2015 (3.67 ± 0.31 chicks) compared with 2016 (2.65 ± 0.26 chicks), due to more total nest failure in 2016 (16/66 = 24%) than in 2015 (5/50 = 10%).

There was a significant year∗treatment interaction for day 17 chick mass ($F_{2,6} = 11.6$, $P = 0.009$) and wing length of nestlings ($F_{2,6} = 11.1$, $P = 0.010$; Table 2). Chick mass at day 17 was independent of treatment in 2015 ($F_{2,33} = 1.96$, $P > 0.15$) but varied with treatment in 2016 ($F_{2,37} = 10.9$, $P < 0.001$): chicks of RT and clipRT females had similar mass ($P > 0.50$) but both were lighter than chicks of control females ($P < 0.01$ in both cases; Table 2).

Similarly, wing length of nestlings was independent of treatment in 2015 ($F_{2,33} = 0.47$, $P > 0.60$) but varied with treatment in 2016 ($F_{2,37} = 12.7$, $P < 0.001$): chicks of RT and clipRT females had shorter wing length in 2016 compared with controls ($P < 0.001$ in both cases; Table 2). For tarsus length, there was no year∗treatment interaction ($F_{2,6} = 1.61$, $P > 0.25$), but there were main effects of treatment ($F_{2,6} = 19.4$, $P = 0.002$) and year ($F_{1,6} = 13.2$, $P = 0.011$). Chicks of RT and clipRT females had similar tarsus length ($P > 0.80$), but both were smaller than chicks of control females ($P < 0.01$ in both cases; Table 2). Overall, chicks had greater tarsus length in 2015 (32.1 ± 0.4 mm) than in 2016 (30.4 ± 0.3 mm).

In 2016, mass loss of females between mid-incubation and the middle of the chick-rearing period varied with handicapping treatment ($F_{2,28} = 6.66$, $P = 0.004$). Mass loss did not differ between control females (2.3 ± 0.4 g, $N = 14$) and RT females (3.7 ± 0.5 g, $N = 10$; $P = 0.13$), but clipRT females lost more mass than both groups of females (4.8 ± 0.5 g, $N = 7$; $P = 0.042$ and $P = 0.001$, respectively).

Provisioning Rate and Nestling Diet for Current (First) Breeding Attempt

Using data from visual behavioural observations, including control birds, there was no effect of treatment on provisioning rate of females ($F_{2,6} = 0.04$, $P > 0.80$) or their male partners ($F_{2,5} = 3.22$, $P = 0.12$; controlling for brood size at day 6; all year and year∗treatment effects: $P > 0.40$; Fig. 1b). Mean provisioning rates for days 6–8 posthatching determined from videos was highly correlated with those determined from behavioural observations for females (Pearson correlation: $r_{37} = 0.74$, $P < 0.001$) and for males ($r_{33} = 0.65$, $P < 0.001$). Provisioning rate increased with chick age, between days 6–8 and days 12–14, in females (3.88 ± 0.77 versus 5.16 ± 0.78 visits/30 min; $t_{33} = 2.78$, $P = 0.00$), but not in males (1.04 ± 0.31 versus 1.60 ± 0.33; $P = 0.10$; treatment and age∗treatment interaction: all $P > 0.18$, controlling for day 6 brood size). Video analysis confirmed there was no overall treatment effect on

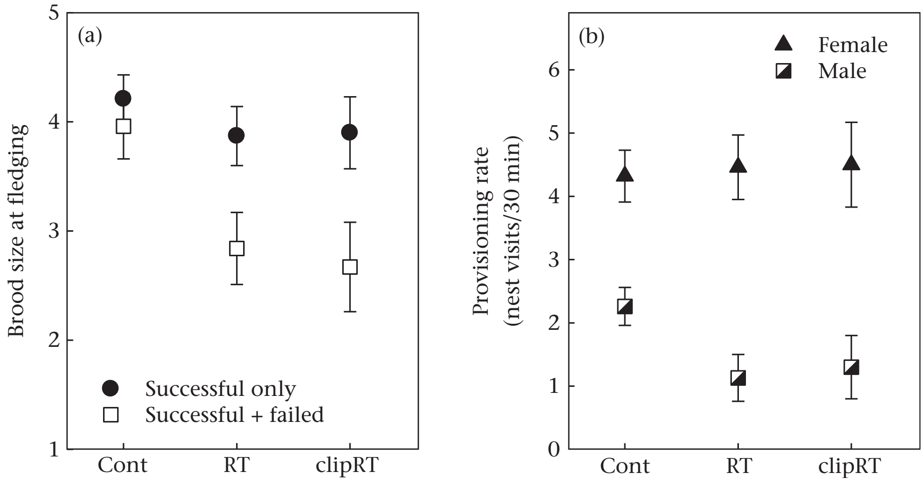

Figure 1. Effect of handicapping treatment on (a) brood size at fledging for the current breeding attempt and (b) provisioning rate (visual observation) of females (days 6–8) and their (nonhandicapped) male partner for 2015 and 2016 combined. Cont = control; RT = radiotransmitter only; clipRT = radio + wing clipping. Values are lsmeans ± SE.

Table 2
Effect of radiotransmitters and wing clipping on chick mass and size at fledging (day 17) for 2015 and 2016 combined

Variable	Year	Experimental treatment		
		Ctrl	RT	ClipRT
Chick fledging mass (g)	2015	73.8 ± 1.1 (19)	77.0 ± 1.3 (12)	76.4 ± 2.1 (5)
	2016	78.6 ± 1.2^{a} (19)	70.2 ± 1.5^{b} (12)	71.5 ± 1.8^{b} (9)
Chick tarsus length (mm)	Pooled	33.1 ± 0.3^{a} (38)	30.3 ± 0.4^{b} (24)	30.4 ± 0.5^{b} (14)
Chick wing length (mm)	2015	88.2 ± 0.8 (19)	88.6 ± 1.1 (12)	90.0 ± 1.6 (5)
	2016	92.9 ± 1.0^{a} (19)	87.1 ± 1.2^{b} (12)	85.1 ± 1.4^{b} (9)

Ctrl = control; RT = radiotransmitter only; clipRT = radio + wing clipping. Values are lsmeans ± SE with number of broods in parentheses. Different superscript letters within rows indicate means differ ($P < 0.05$).

provisioning rate for days 6–8 in females ($P = 0.09$) or males ($P > 0.60$), or on days 12–14 for females ($P > 0.60$) or males ($P > 0.60$; Table 3; treatment∗year interaction $P > 0.80$ in all cases; controlling for day 6 brood size). There was a main effect of year, but only for provisioning rate in females at day 12–14: provisioning rate was higher in 2015 (6.42 ± 0.56 visits/30 min) compared with 2016 (4.23 ± 0.56 visits/30 min; $t_{79} = 2.75$, $P = 0.007$).

Nestling diet data were obtained for a total of 1388 individual meals from video analysis, of which 1335 were single prey-type meals and only 45 (3.3%) were multiple-prey type meals. For the latter, only one meal contained three different prey types and most multiple-prey meals included tipulid larvae (*Tipula paludosa*) + rat-tailed maggots, *Eristalis tenax* ($N = 22$, 49%) or tipulid larvae + -soldier flies, *Hermetia illucens* ($N = 14$, 31%). For simplicity, we restricted subsequent analyses to single prey type (e.g. only tipulid larvae) meals (96.4% of all recorded meals) representing 2648 individual prey items ($N = 2033$ prey from females, $N = 615$ prey from males). There was a significant difference in the overall frequency of main prey items in relation to treatment (Fig. 2).

ClipRT females brought back fewer tipulids (65.4% versus 73.3%) and more soldier flies (15.1% versus 12.1%) and rat-tailed maggots (18.1% versus 13.3%) than RT females ($\chi^2_4 = 16.3$, $P = 0.003$). Male partners of manipulated females showed the opposite pattern: males mated to clipRT females brought back more tipulids (81.4% versus 67.6%) and fewer soldier flies (12.7% versus 26.3%; $\chi^2_4 = 19.2$, $P < 0.001$) than mates of RT females. However, there was no effect of treatment on the number of prey brought back to the nest. On average, RT females brought back 11.1 ± 4.4 prey items/30 min, whereas clipRT females brought back 12.9 ± 6.2 prey items/30 min ($F_{1,34} = 0.99$, $P = 0.32$).

Activity During the Current (First) Breeding Attempt

There was a significant breeding stage∗treatment interaction for activity ($F_{3,732} = 4.34$, $P = 0.005$; Fig. 3). Activity was higher in RT females during chick rearing (36.2 ± 5.6%) compared with clipRT females (28.5 ± 5.7; $t_{732} = 4.37$, Bonferroni-corrected $P < 0.001$), but there was no effect of treatment for incubation, brooding and postfledging stages ($P > 0.4$ in all cases).

Table 3
Effect of radiotransmitters and wing clipping on provisioning rate (nest visits/30 min) of female European starlings and their male partners (using data from videos) for 2015 and 2016 combined

Chick age	Bird sex	RT	ClipRT
Day 6–8	Female	4.49 ± 0.43	3.33 ± 0.53
	Male	0.93 ± 0.24	1.01 ± 0.29
Day 12–14	Female	5.15 ± 0.48	5.50 ± 0.61
	Male	1.63 ± 0.44	1.91 ± 0.58

RT = radiotransmitter only; clipRT = radio + wing clipping. Values are lsmeans ± SE.

We then restricted analysis to the chick-rearing period from day 6 (postbrooding) to day 21 (fledging) and analysed activity by year, treatment and day, controlling for number of observations (with band as a random effect). Treatment varied with day ($F_{15,285} = 1.98$, $P = 0.017$; Fig. 4), but no two- or three-way interactions were significant in the model ($P > 0.25$ in all cases). However, there was a main effect of treatment ($F_{1,285} = 8.59$, $P = 0.004$) and year ($F_{1,285} = 21.8$, $P < 0.001$) on overall activity. During days 6–21 of chick rearing, clipRT females were 22% less active than control females (29.2 ± 2.5% versus 37.1 ± 1.8% active detections) and, on average, activity was higher in 2015 (39.2 ± 2.4%) than in 2016 (27.1 ± 1.8%).

Despite marked variation in activity among chick-rearing females (32.8 ± 8.2%, $N = 30$, range 17.9–48.7%), brood size at

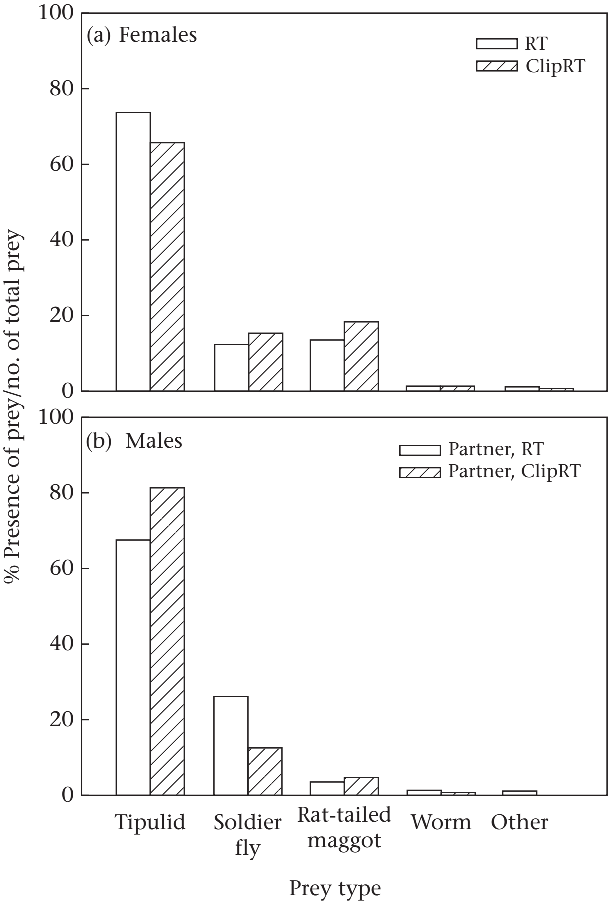

Figure 2. Effect of the handicapping treatment on the number and type of prey delivered to the nest by (a) females and (b) their (nonhandicapped) male partner for 2015 and 2016 combined. RT = radiotransmitter only; clipRT = radio + wing clipping. Bars indicate percentage of total prey items.

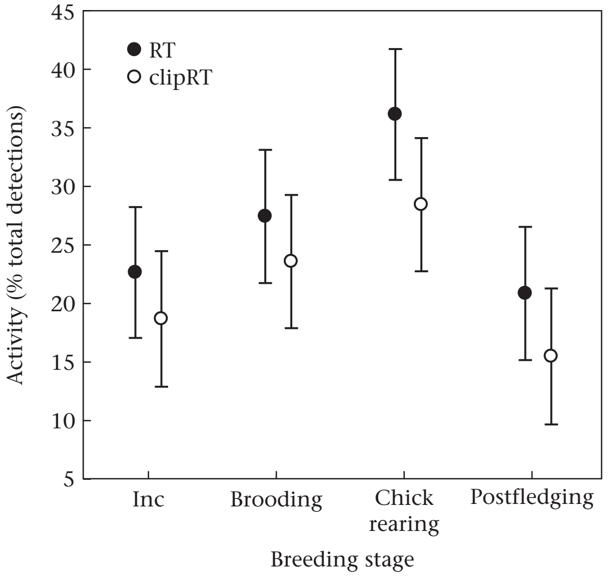

Figure 3. Total activity (% total detections with Δ power > threshold) in relation to handicapping treatment and breeding stage (incubation, brooding, chick rearing, postfledging) in females for 2015 and 2016 combined. RT = radiotransmitter only; clipRT = radio + wing clipping. Values are lsmeans ± SE.

fledging, chick mass at fledging and female provisioning rate (days 6–8) were all independent of activity ($P > 0.30$ in all cases; all treatment and treatment∗activity interactions: $P > 0.20$). Overall activity during chick rearing was similar for females that did (32.0 ± 3.2%) and did not (34.0 ± 3.3%; $F_{1,25} = 0.42$, $P > 0.50$) initiate a second brood (no effect of treatment and interaction: $P > 0.39$). Similarly, activity did not differ between females that did (36.5 ± 3.6%) and did not (30.7 ± 3.3%; $F_{1,25} = 3.80$, $P = 0.062$) return in the subsequent year (no effect of treatment or interaction: $P > 0.22$). Finally, variation in overall activity during chick rearing did not explain variation in cumulative number of chicks fledged over 2 years ($F_{1,25} = 0.01$, $P > 0.90$).

Future Costs of Handicapping Treatment

Both year 1 breeding productivity ($F_{2,16} = 55.1$, $P < 0.001$) and 2-year cumulative productivity ($F_{2,16} = 22.1$, $P < 0.001$) were dependent on nest fate in the first breeding attempt. Overall, birds that abandoned their first (manipulated) breeding attempt before hatching had very low annual and 2-year cumulative breeding productivity (0.46 ± 0.53 chicks and 0.64 ± 1.04 chicks, respectively), i.e. these birds did not ‘recover’ productivity through laying replacement clutches or breeding in the following year (e.g. only 1/16 birds that abandoned initiated a second brood in the same year). Females that failed posthatching during their first breeding attempt also had low annual breeding productivity (0.95 ± 0.46 chicks) but higher 2-year productivity (2.89 ± 0.90 chicks) because more of these birds returned and bred successfully in year 2. Since females that abandoned did not incur the cost of experimentally manipulated workload during rearing of a first brood (and possibly abandoned due to an immediate handling effect), we restricted subsequent analysis to successful and failed birds ($N = 100$).

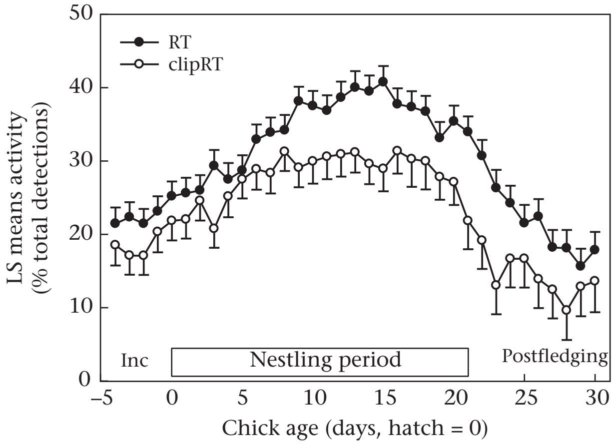

Figure 4. Variation in total activity (% total detections with Δ power > threshold) for female parents in relation to chick age (hatch = day 0) from late incubation to the postfledging period for 2015 and 2016 combined. RT = radiotransmitter only; clipRT = radio + wing clipping. Values are lsmeans ± SD.

Table 4 provides results for the effect of handicapping on measures of future fecundity and local return rate, including and excluding birds that hatched chicks but failed before fledging in their first breeding attempt.

‘Year’ was not significant in any models as a main effect (Table 4), so we included year as a random factor (models without ‘year’ gave the same results). Treatment had no effect on the probability of initiating a second brood in the same year among successful birds ($\chi^2_3 = 2.23$, $P < 0.50$), but when including failed birds, both RT and clipRT females were less likely to initiate a second brood compared with control females ($\chi^2_2 = 6.01$, $P = 0.040$). Brood size at fledging for second broods was independent of treatment ($P > 0.07$ in both cases; Table 4). Treatment had an effect on local return rate for successful birds ($\chi^2_2 = 7.17$, $P = 0.028$) and failed + successful birds ($\chi^2_2 = 10.8$, $P = 0.005$). RT females had lower return rates than controls, with clipRT females having intermediate return rates among successful females but lower return rates equal to those of RT females when failed birds were included (Table 4). Treatment affected future productivity ($F_{2,13} = 10.0$, $P = 0.002$) and cumulative 2-year productivity ($F_{2,13} = 13.2$, $P < 0.001$) among successful females: RT and clipRT females both fledged fewer chicks than did controls, but these two treatments did not differ (the same result was obtained including failed birds; Table 4). Therefore, overall, there were no significant differences between RT females and clipRT females for any measure of future fecundity or return rate (Table 4).

DISCUSSION

In this study, we experimentally increased workload of female European starlings during chick rearing, handicapping birds with a radiotransmitter with or without wing clipping, and analysed their corresponding change in total diurnal activity using a novel automated radiotracking system. Overall, handicapping decreased current breeding success due to higher abandonment immediately after treatment. Among successful and failed birds (birds that incubated chicks at least to hatch), handicapping reduced current breeding success. However, among successful birds (fledging ≥ 1 chick), there was no effect of handicapping on brood size at fledging for the current breeding attempt, i.e. any effect of handicapping was due to complete breeding failure. Chicks of handicapped females had shorter tarsi and decreased mass and wing length but only in one of two years (2016), and there was no evidence of an additive effect of wing clipping on chick size and mass. We detected no effect of treatment on levels of parental care for the first brood based on provisioning rate. In contrast, there was an effect of treatment on total activity measured using automated radiotracking: during chick rearing, but not at other breeding stages, wing-clipped females had 22% lower activity compared to females with radios only. In addition, handicapped females brought back

Table 4
Effect of handicapping on future fecundity and survival (local return rate) for females captured in 2015 and 2016 combined

Variable	Year	Experimental treatment		
		Ctrl	RT	clipRT
Successful birds during first breeding attempt				
Initiating 2nd brood (%)	NS	71.8% (39)	58.3% (24)	56.3% (16)
Brood size at fledging − 2nd brood	NS	2.48 ± 0.32 (28)	1.64 ± 0.44 (14)	0.67 ± 0.53 (10)
Local return rate (%)	NS	64.1% (39)^{a}	29.2% (24)^{b}	43.8% (16)^{ab}
Future productivity (brood 2 and year 2)	NS	5.32 ± 0.65^{a} (39)	2.12 ± 1.01^{b} (24)	1.68 ± 0.82^{b} (16)
Cumulative no. chicks fledged (2 years)	NS	9.41 ± 0.71^{a} (39)	5.58 ± 0.89^{b} (24)	5.92 ± 1.07^{b} (16)
Failed + successful birds during first breeding attempt				
Initiating 2nd brood (%)	NS	69.1% (42)^{a}	42.9% (35)^{b}	43.5% (23)^{b}
Brood size at fledging − 2nd brood	NS	2.53 ± 0.31 (29)	1.61 ± 0.43 (15)	0.82 ± 0.50 (11)
Local return rate (%)	NS	66.7% (42)^{a}	31.4% (35)^{b}	34.8% (23)^{ab}
Future productivity (brood 2 and year 2)	NS	5.44 ± 0.60^{a} (42)	2.25 ± 0.80^{b} (35)	1.74 ± 0.70^{b} (23)
Cumulative no. chicks fledged (2 years)	NS	9.10 ± 0.80^{a} (42)	4.42 ± 0.83^{b} (35)	5.00 ± 1.00^{b} (23)

Ctrl = control; RT = radiotransmitter only; clipRT = radio + wing clipping. Values are percentages (%) or lsmeans ± SE with number of females/broods in parentheses. Different superscript letters within rows indicate means differ ($P < 0.05$).

fewer tipulids and more black soldier flies and rat-tailed maggots. The effect of handicapping on future fecundity was mainly associated with differences in nest failure: including failed birds, both RT and clipRT females had a lower probability of initiating a second brood, fledged fewer chicks overall in year 1 and had a lower return rate, compared with controls. Still, among successful birds, local return rate and future productivity were lower in both the RT and clipRT treatments, but with no evidence for additive costs of wing clipping.

In our study, therefore, handicapping had few consistent effects on parental investment, breeding productivity or chick size and mass in the current breeding attempt among successful females: the main effect of treatment occurred due to higher abandonment or early nest failure (see also Hegemann et al., 2013; Rivers et al., 2017). Previous studies have reported mixed effects of handicapping on parental investment and current productivity; several studies reported decreased provisioning rate in handicapped individuals (Barron et al., 2013; Tieleman, Dijkstra, Klasing, Visser, & Williams, 2008; Winkler & Allen, 1995; Wright et al., 1998), but other studies report no effect of handicapping on provisioning rate (Fowler & Williams, 2017; Neudorf & Pitcher, 1997; Rivers et al., 2017). Most studies have found no effect of handicapping on the number of chicks fledged or chick size and mass even where provisioning rate decreased (e.g. Slagsvold & Lifjeld, 1988; Winkler & Allen, 1995; but see Barron, 2013; Wright et al., 1998). In part, these seemingly contradictory results might be explained by different handicapping methods, e.g. radiotransmitters versus clipping, manipulation before or after hatching, handicapping one or both birds of a pair. However, an equally parsimonious explanation is that, as predicted by life-history theory, parents should adjust the trade-off between self-maintenance and investment in current offspring depending on ecological context (e.g. year-specific resource availability) and/or their physiological state. Thus, we should expect different results of handicapping and increasing demands of parental care in different years, even with a standard experimental manipulation (Hegemann et al., 2013; Williams, 2018). We found some evidence for such year-specific effects in our study. There was higher nest abandonment, smaller chick fledging mass/size and lower overall female provisioning rate (independent of treatment) 12–14 days posthatching in 2016, suggesting this was a ‘poorer’ year. In an earlier study at our study site using a similar wing-clipping approach, Fowler and Williams (2017) did find that clipRT females had lower current productivity in a year when handicapped females showed clear evidence of a physiological cost of reproduction. In 2016 there was no effect of handicapping on physiological traits of females during parental care (Williams, 2018). This confirms that year-specific differences in how birds respond to increased demands of parental care, under different ecological contexts, are manifest at both a behavioural and physiological level (see also Mathot et al., 2017).

We predicted an increase in costs of reproduction if our manipulation caused an additive increase in costs of activity, i.e. increased wing loading causing an increase in costs of flight: control < RT < clipRT. We found clear evidence for a negative effect of handicapping on measures of future fecundity (lower probability of initiating a second brood, fewer chicks fledge from subsequent breeding attempts) and return rate, consistent with an increase in costs of reproduction. However, contrary to our prediction, we found little evidence for an additive effect of wing clipping over just radio attachment. Among successful birds, both RT and clipRT females had a lower cumulative number of chicks fledged over 2 years compared with controls, and although RT females had lower return rates than controls, clipRT females had a higher, intermediate, return rate. Although radiotransmitters are often viewed as inconsequential, a meta-analysis of radiotransmitter effects on avian behaviour and ecology found negative effects on 8 out of 12 aspects analysed (Barron et al., 2010). Still, few previous handicapping studies have measured effects on future fecundity (see Barron et al., 2010, for transmitter studies). However, in a study of handicapped skylarks, *Alauda arvensis*, Hegemann et al. (2013) suggested that parents shifted the balance between self-maintenance and nest success between first and second broods. Costs of handicapping were manifest in offspring of first broods (lower chick size and mass) whereas parents had lower physiological condition in second broods (Hegemann et al., 2013). More studies have investigated effects of handicapping on survival, but results are also mixed. In some studies, wing-clipped birds did not have lower return rates, perhaps because in these studies birds reduced their provisioning rate to chicks and had lower productivity in their current breeding attempt (Bijleveld & Mullers, 2009; Slagsvold & Lifjeld, 1988; Wright et al., 1998). However, in other studies, wing-clipped birds did have lower return rates whether they maintained (Winkler & Allen, 1995) or reduced (Jacobs et al., 2013; Love & Williams, 2008) current productivity.

One reason for the mixed results of handicapping studies, and for the lack of an additive effect of wing clipping in our study, is that birds might use different ‘strategies’ to deal with increasing costs of activity during parental care. Some studies have found a decrease in mass loss following wing-clipping treatment (Velando, 2002; Weimerskirch et al., 1995; Winkler & Allen, 1995), although other studies have reported no change in mass (Velando & Alonso-Alvarez, 2003; Weimerskirch, Fradet, & Cherel, 1999). Parental mass loss itself should reflect a trade-off between lower costs of flight, due to lower wing loading (Lind & Jakobsson, 2001; Norberg, 1981), and some increased risk to self-maintenance or survival, and this trade-off likely varies under different ecological contexts (e.g. in different years; Williams, 2018). Although we only measured the change in body mass (from mid-incubation to mid-chick rearing) in one year, wing-clipped females lost more than twice as much mass between incubation and mid-chick rearing as control and radio-only females. Although mass loss is often assumed to reflect a cost, we found no evidence for physiological costs of reproduction in females in 2016 (Williams, 2018; cf. Fowler & Williams, 2017). Thus, we suggest that greater mass loss in wing-clipped females reduced their wing loading and reduced the effect of handicapping on future fecundity and survival (see Fowler & Williams, 2017).

Handicapping had no effect on provisioning rate or on the number of prey brought back per nest visit for the current brood in either sex. However, clipRT females brought back fewer tipulids and more soldier flies and rat-tailed maggots than did RT females. European starlings are typically considered to be diet specialists during the breeding season, relying on soil-dwelling larvae taken from pastures, mown fields and lawns (Feare, 1984; Tinbergen, 1981) with Tipulidae (especially *T. paludosa*) being a key resource for provisioning young (Dunnet, 1955; Rhymer, Devereux, Denny, & Whittingham, 2012; Tinbergen, 1981). Soldier flies have a lower energy content per gram than tipulid larvae (Bell, 1990), so our results are consistent with Wright et al.'s (1998) finding that European starlings feeding experimentally enlarged broods deliver a lower proportion of tipulid larvae and more, lower-quality prey items (earthworms and pig pellets). However, we also found that male partners of handicapped females showed the opposite pattern, with males mated to clipRT females bringing back more tipulids and fewer soldier flies. Here, males may be altering their behaviour to compensate for their handicapped partners (Griggio, Matessi, & Pilastro, 2005). However, in a different study on the same site, there was no difference in brood size at fledgling when males did or did not contribute to provisioning offspring (Fowler & Williams, 2015). Thus, handicapping likely had little effect on overall nestling diet quality per nest, consistent with the small effects on brood size at fledging and offspring quality.

However, our automated telemetry data suggest that birds can also use an alternative strategy to modulate any costs of increased workload generated by handicapping. We suggest that, in our study, wing-clipped females compensated for increased costs of flight associated with central place foraging (based on nest visit rate) by decreasing some (unknown) aspect of their overall activity, allowing them to modulate costs of reproduction. Our telemetry data show that, in general, females were less active during incubation and that activity increased markedly during chick rearing, consistent with previous studies (Tinbergen, 1981, based on $N = 1$ female; Feare, 1984). However, we also found that female activity during brooding on days 1–5 after hatching was intermediate between activity during incubation and chick rearing, and that activity of females decreased during the postfledging period. Female European starlings that double-brood initiate egg laying within 0–3 days of the first brood fledging, so this supports Kessel's (1957) assertion that females contribute less than males to postfledging care of offspring. In our study, during breeding stages with overall lower activity (incubation, brooding and postfledging), there was no effect of handicapping on female activity. However, during the main chick-rearing phase, wing-clipped females had 22% lower activity than radio-only females. Interestingly, our measure of total activity was not correlated with behaviour directly related to parental care (provisioning rate, number of prey, prey type) or the outcome of behaviour directed towards parental care (brood size, chick size, mass). This suggests that our measure of total activity is capturing components of an individual's behaviour not directly related to chick rearing, e.g. changes in activity directed at self-maintenance, which in turn allow wing-clipped females to modulate costs of handicapping in terms of costs of reproduction. Automated radiotelemetry has the potential to capture aspects of parental care behaviour that are difficult to observe directly. To our knowledge, our study is the first to use activity, calculated from an automated radiotelemetry system, to quantify parental care workload. Given the variety of ways in which individuals can modify their behaviour when faced with an increased workload, automated radiotracking offers a unique ability to capture overall activity of behaviours occurring at the nest as well as away from the nest. Our study provides an explanation for the often contradictory effects of handicapping reported on reproductive effort and costs of reproduction: individuals can use behavioural flexibility – decreasing overall activity while maintaining provisioning rate – along with changes in mass and nestling diet to mitigate putative effects of increased workload imposed by handicapping. However, this change in behaviour may come at a cost to self-maintenance such that increased workload still results in a decreased ability to initiate a second brood, a decrease in future fecundity and a decrease in survival. Future studies should focus on the detailed components of behaviour during parental care, not just flight associated with central place foraging, to identify specific mechanisms of parental flexibility for dealing with variable demands and costs during chick rearing (Killen, Calsbeek, & Williams, 2017; Mathot et al., 2017; Williams, 2018).

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Supplementary data

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