

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

Mitchell W. Serota ^{*}, Tony D. Williams

Department of Biological Sciences, Simon Fraser University, Burnaby, BC, Canada

a r t i c l e i n f o

Article history:

Received 14 September 2018

Initial acceptance 22 October 2018

Final acceptance 6 November 2018

Available online 28 December 2018

MS. number: A18-00667R

Keywords:

activity

automated telemetry

costs of reproduction

handicapping

parental care

no change in provisioning rate or the number of chicks reared (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 e 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 al-

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

provisioning rate for days 6 e 8 in females ($P \geq 0.09$) or males ($P > 0.60$), or on days 12 e 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 e 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

edging, chick mass at edging and female provisioning rate (days 6e 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 ($32.0 \pm 3.2\%$) and did not ($34.0 \pm 3.3\%$; $F_{1,25} = 0.42$, $P > 0.50$) initiate a second brood (no effect of treatment and interaction: $P > 0.39$). Similarly, activity did not differ between females that did

mass loss itself should re

- Griggio, M., Matessi, G., & Pilastro, A. (2005). Should I stay or should I go? Female brood desertion and male counter-strategy in rock sparrows. *Behavioral Ecology*, 16, 435e 441.
- Hegemann, A., Matson, K., Flins, H., & Tieleman, B. (2013). Offspring pay sooner, parents pay later: Experimental manipulation of body mass reveals trade-offs between immune function, reproduction and survival. *Frontiers in Zoology*, 10, 77. <https://doi.org/10.1186/1742-9994-10-77> .
- Jacobs, S. R., Elliott, K. H., & Gaston, A. J. (2013). Parents are a drag: Long-lived birds share the cost of increased foraging effort with their offspring, but males pass on more of the costs than females. *PLoS One*, 8, e54594. <https://doi.org/10.1371/journal.pone.0054594> .
- Kessel, B. (1957). A study of the breeding biology of the European starling (*Sturnus vulgaris* L.) in North America. *American Midland Naturalist*, 58, 257e 331.
- Killen, S. S., Calsbeek, R., & Williams, T. D. (2017). The ecology of exercise: Mechanisms underlying individual variation in behaviour, activity, and performance: An introduction to symposium. *Integrative and Comparative Biology*, 57, 185e 194.
- Lind, J., & Jakobsson, S. (2001). Body building and concurrent mass loss: Flight adaptations in tree sparrows. *Proceedings of the Royal Society B: Biological Sciences*, 268, 1915e 1919.
- Love, O. P., & Williams, T. D. (2008). The adaptive value of stress-induced phenotypes: Effects of maternally derived corticosterone on sex-biased investment, cost of reproduction, and maternal fitness. *American Naturalist*, 172, E135e E149.
- Mariette, M. M., Pariser, E. C., Gilby, A. J., Magrath, M. J. L., Pryke, S. R., & Griffith, S. C. (2011). Using an electronic monitoring system to link offspring provisioning and foraging behaviour of a wild passerine. *Auk*, 128, 26e 35.
- Mathot, K. J., Olsen, A.-L., Mutzel, A., Araya-Ajoy, Y. G., Nicolaus, M., Westneat, D. F., et al. (2017). Provisioning tactics of great tits (*Parus major*) in response to long-term brood size manipulations differ across years. *Behavioral Ecology*, 28, 1402e 1413.
- Moreno, J., Cowie, R. J., Sanz, J. J., & Williams, R. S. R. (1995). Differential response by males and females to brood manipulations in the pied flycatcher: Energy expenditure and nestling diet. *Journal of Animal Ecology*, 64, 721e 732.
- Neudorf, D. L., & Pitcher, T. E. (1997). Radio transmitters do not affect nestling feeding rates by female hooded warblers. *Journal of Field Ornithology*, 68, 64e 68.
- Norberg, R. A. (1981). Temporary weight decrease in breeding birds may result in more fledged young. *American Naturalist*, 118, 838e 850.
- Rappole, J., & Tipton, A. (1991). New harness design for attachment of radio transmitters to small passerines. *Journal of Field Ornithology*, 62, 335e 337.
- Rhymer, C. M., Devereux, C. L., Denny, M. J. H., & Whittingham, M. J. (2012). Diet of starling *Sturnus vulgaris* nestlings on farmland: The importance of Tipulidae larvae. *Bird Study*, 59, 426e 436.
- Rivers, J. W., Newberry, G. N., Schwarz, C. J., & Ardia, D. R. (2017). Success despite the stress: Violet-green swallows increase glucocorticoids and maintain reproductive output despite experimental increases in flight costs. *Functional Ecology*, 31, 235e 244.
- Royle, N. J., Smiseth, P. T., & Kolliker, M. (2012). *The evolution of parental care*. Oxford, U.K.: Oxford University Press.
- Santos, E. S. A., & Nakagawa, S. (2012). The costs of parental care: A meta-analysis of the trade-off between parental effort and survival in birds. *Journal of Evolutionary Biology*, 25, 1911e 1917.
- Schwagmeyer, P. L., & Mock, D. W. (2008). Parental provisioning and offspring fitness: Size matters. *Animal Behaviour*, 75, 291e 298.
- Slagsvold, T., & Lifjeld, J. T. (1988). Ultimate adjustment of clutch size to parental feeding capacity in a passerine bird. *Ecology*, 69, 1918e 1922.
- Stauss, M. J., Burkhardt, J. F., & Tomiuk, J. (2005). Foraging flight distances as a measure of parental effort in blue tits *Parus caeruleus* differ with environmental conditions. *Journal of Avian Biology*, 36, 47e 56.
- Stearns, S. C. (1992). *The evolution of life-histories*. Oxford, U.K.: Oxford University Press.
- Steiger, S. S., Valcu, M., Spoelstra, K., Helm, B., Wikelski, M., & Kempenaers, B. (2013). When the sun never sets: Diverse activity rhythms under continuous daylight in free-living Arctic-breeding birds. *Proceedings of the Royal Society B: Biological Sciences*, 280, 20131016. <https://doi.org/10.1098/rspb.2013.1016> .
- Tieleman, B. I., Dijkstra, T. H., Klasing, K. C., Visser, G. H., & Williams, J. B. (2008). Effects of experimentally increased costs of activity during reproduction on parental investment and self-maintenance in tropical house wrens. *Behavioral Ecology*, 19, 949e 959.
- Tinbergen, J. M. (1981). Foraging decisions in starlings (*Sturnus vulgaris*). *Ardea*, 69, 1e 67.
- Velando, A. (2002). Experimental manipulation of maternal effort produces differential effects in sons and daughters: Implications for adaptive sex ratios in the blue-footed booby. *Behavioral Ecology*, 13, 443e 449.
- Velando, A., & Alonso-Alvarez, C. (2003). Differential body condition regulation by males and females in response to experimental manipulations of brood size and parental effort in the blue-footed booby. *Journal of Animal Ecology*, 72, 846e 856.
- Ward, M. P., Alessi, M., Benson, T. J., & Chiavacci, S. J. (2014). The active nightlife of diurnal birds: Extraterritorial forays and nocturnal activity patterns. *Animal Behaviour*, 88, 175e 184.
- Weimerskirch, H., Chastel, O., & Ackermann, L. (1995). Adjustment of parental effort to manipulated foraging ability in a pelagic seabird, the thin-billed prion *Pachyptila belcheri*. *Behavioral Ecology and Sociobiology*, 36, 11e 16.
- Weimerskirch, H., Fradet, G., & Cherel, Y. (1999). Natural and experimental changes in chick provisioning in a long-lived seabird, the Antarctic prion. *Journal of Avian Biology*, 30, 165e 174.
- Williams, T. D. (2012). *Physiological adaptations for breeding in birds*. Princeton, NJ: Princeton University Press.
- Williams, T. D. (2018). Physiology, activity and costs of parental care in birds. *Journal of Experimental Biology*, 221, jeb169433. <https://doi.org/10.1242/jeb.169433> .
- Wilmers, C. C., Nickel, B., Bryce, C. M., Smith, J. A., Wheat, R. E., & Yovovich, V. (2015). The golden age of bio-logging: How animal-borne sensors are advancing the frontiers of ecology. *Ecology*, 96, 1741e 1753.
- Winkler, D. W., & Allen, P. E. (1995). Effects of handicapping on female condition and reproduction in tree swallows (*Tachycineta bicolor*). *Auk*, 112, 737e 747.
- Wright, J., Both, C., Cotton, P. A., & Bryant, D. M. (1998). Quality vs. quantity: Energetic and nutritional trade-offs in parental provisioning strategies. *Journal of Animal Ecology*, 67, 620e 634.
- Wright, J., & Cuthill, I. (1989). Manipulation of sex differences in parental care. *Proceedings of the Royal Society B: Biological Sciences*, 236, 1261-1266.
- Zúñiga, D., Falconer, J., Fudickar, A. M., Jensen, T., Tipton, A., Schmitz, C., et al. (2015). Parental investment in offspring: The role of parental effort and offspring quality. *Journal of Animal Ecology*, 84, 1253-1261.