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Short communication

The effects of force-fledging and premature fledging on the survival of nestling songbirds

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Despite the broad consensus that force-fledging of nestling songbirds lowers their probability of survival and therefore should be generally avoided by researchers, that presumption has not been tested. We used radiotelemetry to monitor the survival of fledglings of Ovenbirds *Seiurus aurocapilla* and Golden-winged Warblers *Vermivora chrysoptera* that we unintentionally force-fledged (i.e. nestlings left the nest in response to our research activities at typical fledging age), that fledged prematurely (i.e. nestlings left the nest earlier than typical fledging age), and that fledged independently of our activities. Force-fledged Ovenbirds experienced significantly higher survival than those that fledged independent of our activities, and prematurely fledged Ovenbirds had a similarly high survival to those that force-fledged at typical fledging age. We observed a similar, though not statistically significant, pattern in Golden-winged Warbler fledgling survival. Our results suggest that investigator-induced force-fledging of nestlings, even when deemed premature, does not necessarily result in reduced fledgling survival in these species. Instead, our results suggest that a propensity or ability to fledge in response to disturbance may be a predictor of a higher probability of fledgling survival.

Keywords: breeding ecology, fledgling survival, Golden-winged Warbler, observer effects, Ovenbird, *Seiurus aurocapilla*, *Vermivora chrysoptera*.

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Many studies of nesting passerines use different methods late in the nestling stage from those used earlier in the nestling stage to avoid the negative impacts of force-fledging or prematurely fledging young from nests (e.g. Anderson & Anderson 1961, Bjornstad & Lifjeld 1996, Holmes *et al.* 1996, Payne & Payne 1998, Sillet *et al.* 2000, Ferretti *et al.* 2005, Maddox & Weatherhead 2008). Although the terms are often used interchangeably, we use 'force-fledging' to refer to nestlings leaving the nest in response to investigator stimulus, and 'premature fledging' as force-fledging that occurs prior to typical fledging age. Although the term fledge technically refers to the developmental stage at which young birds first fly, it is used ubiquitously in the songbird literature to refer to leaving the nest (i.e. fledging from the nest; Gill 1995), and we maintain the latter common definition here. Anecdotal evidence of detrimental effects of force-fledging and premature fledging dates back more than 100 years, when Cole (1910) reported finding ringed nestlings dead outside nests. Cole (1910) subsequently stated that observing dead nestlings outside nests, regardless of researcher activities, 'is not an uncommon thing', and concluded that no causal relationship could be drawn between nestling handling and mortality in those cases. Cole nevertheless concluded that premature-fledging is 'probably, however, the greatest danger to the birds from our work'. Recently, Pietz *et al.* (2012) reiterated that warning: 'We echo Cole's (1910) advice from a century ago that researchers who handle older nestlings (e.g. to measure or band) need to be aware of their possible impacts.' Yet Pietz *et al.* (2012) conceded that the fates of force-fledged or prematurely fledged birds are rarely known. We are not aware of any empirical studies of the impacts of force-fledging or premature fledging on songbirds despite widespread attempts to avoid it (e.g. Ezaki 1988, Briskie 1995, Brooke & Nakamura 1998, Confer *et al.* 2003, Nagy & Holmes 2005, Ardia 2006) on the assumption that it results in reduced fledgling survival (e.g. Hamilton & Martin 1985, Miller & Leonard 2010, Ball & Bayne 2012).

We examined the impact of force-fledging at typical fledging age and premature fledging on fledgling survival in Ovenbirds *Seiurus aurocapilla* and Golden-winged Warblers *Vermivora chrysoptera* in the western Great Lakes region, USA and Canada. We did not purposefully force any nestlings to fledge, but some broods did not remain in nests after our ringing and transmitter attachment activities, which provided an ideal opportunity to test the assumption that force-fledging and premature fledging caused by investigator activities negatively affect fledgling survival. We compared survival of fledglings that left nests independently of our activities within 3 days of marking, those that force-fledged (nestlings would not stay in nest after handling at typical fledging age) and those that prematurely fledged (nestlings would not stay in nest after handling those younger than typical fledging age).

METHODS

As part of separate studies of population ecology, we searched for and monitored Ovenbird nests during 2007 and 2008 in the Chippewa National Forest (47°31′N, 94°16′W) in north-central Minnesota, and Golden-winged Warbler nests during 2011 and 2012 in Tamarac National Wildlife Refuge (NWR; 47°2′N, 95°35′W) in northwest Minnesota, Rice Lake NWR (46°31′N, 93°20′W) in east-central Minnesota, and Sandilands Provincial Forest (PF; 49°39′N, 96°15′W) in southeast Manitoba. We located nests of both species using methods modified from Martin and Geupel (1993), including monitoring parental activity and systematic searching. We also located Golden-winged Warbler nests by netting and attaching radio-transmitters to females and radiotracking them through the breeding season. We visited nests every 4 days, or more often when we expected stage transitions (i.e. onset of incubation and hatching) to confirm ages of nestlings and to predict expected fledging dates.

Nestlings in our study populations typically fledge on day 8 (Ovenbirds) and day 8 or 9 (Golden-winged Warblers) of the nestling stage, where hatching day is day 1. However, some Ovenbirds fledge on days 7 or 9, and some Golden-winged Warblers fledge on days 7, 10 and, rarely, 11. On day 7 of the nestling stage for both species in Minnesota, we removed broods from nests (mean brood size was 4.2 for Ovenbirds and 4.4 for Golden-winged Warblers), ringed all nestlings with U.S. Geological Survey aluminium leg rings, and attached radio-transmitters to one to two (Ovenbirds) and one to five (Golden-winged Warblers) nestlings using a figure-eight harness design modified from Rappole and Tipton (1991). Due to logistical constraints, bad weather or finding nests at late stages, we sometimes attached transmitters on days 8–10. In Sandilands PF, we attempted to attach transmitters to Golden-winged Warblers on day 6 in an effort to avoid premature fledging and its presumed negative consequences for this species protected under Canada's Species at Risk Act. However, for the reasons stated above and because birds were sometimes too small to fit with transmitters on day 6, we often marked Manitoba birds on day 7 and sometimes day 8.

We removed nestlings from nests for ringing and transmitter attachment and replaced each brood in its nest within 15 min. When nestlings remained in the nest (84% of broods from 179 nests), we observed them for 3–5 min from a distance of > 5 m, and checked many nests (*c.* 50%) 30–60 min after handling to confirm that nestlings had not fledged. We also monitored some (*c.* 5%) nests with digital video cameras for up to 3 days after handling nestlings. We did not observe evidence of any broods fledging between 1 min and 1 h after handling. Therefore, we considered those broods that fledged within the first minute after handling to have fledged in response to our activities. We considered all other broods to have fledged naturally, although certainly some of those broods could have been force-fledged by other stimuli (e.g. predators). Although some small percentage (< 10% in our study) of Ovenbirds and Golden-winged Warblers fledge on day 7 in the absence of force-fledging, we considered any brood that we force-fledged on day 7 to have fledged prematurely. In the first few cases of force-fledging Ovenbirds in 2007, we attempted to gather the birds and replace them in the nest, but they immediately jumped back out. In all other cases of force-fledging or premature fledging in both species, we immediately left the area and did not attempt to gather and replace fledglings into the nest. At three Golden-winged Warbler nests, we prematurely fledged partial broods (i.e. some nestlings force-fledged on day 7 and others remained in the nest). In each case, the remaining nestlings would have been included as fledging independent of our activities, but they were subsequently depredated before fledging. We used radiotelemetry to monitor the fate (i.e. survival or mortality) of each radiomarked fledgling once a day for 24 days, the approximate age of independence from adult care for each species (Streby & Andersen 2011, H.M. Streby unpubl. data).

Statistical analysis

We compared survival among force-fledged, prematurely fledged and apparently naturally fledged Ovenbird and Golden-winged Warbler fledglings. For each group, we calculated daily survival from coefficients of a logistic exposure model (Shaffer 2004). All models included a random effect for brood, because survival among siblings was unlikely to be independent. In addition, all models included a quadratic term for fledgling age because survival clearly increased non-linearly with fledgling age. We calculated the probability of a fledgling in each group surviving to independence as the product of daily survival probabilities for days 1–24. We used Z-tests to compare survival estimates, and we considered tests significant if $Z > 1.96$, equivalent to $a = 0.05$.

RESULTS

We monitored 90 fledgling Ovenbirds from 83 broods and 227 fledgling Golden-winged Warblers from 96 broods. Of those 317 individuals monitored, six fledglings from four (5%) Ovenbird broods and 18 fledglings from 12 (12%) Golden-winged Warbler broods were force-fledged on day 8 or 9, and nine nestlings from nine (11%) Ovenbird broods and eight nestlings from seven (7%) Golden-winged Warbler broods (four whole broods and three partial broods) fledged on day 7 and were considered to have fledged prematurely. In all three cases in which partial broods prematurely fledged, the fledglings we monitored (n = 3) survived to independence from adult care, whereas the remaining radio-marked nestlings (n = 5) were predated in their nests within 24 h of handling and marking with rings and transmitters. Nestling mortalities were not included in the comparison of fledgling survival.

Ovenbirds that force-fledged as a result of being handled experienced higher survival than those that fledged independently of our activities, and those that prematurely fledged experienced similar survival to force-fledged birds, but not significantly higher survival than those that fledged independently of our activities (Fig. 1). Fledgling Golden-winged Warbler survival followed a similar pattern, but the differences were not statistically significant (Fig. 1).

None of the birds we force-fledged or prematurely fledged died from exposure, whereas one (2%) Ovenbird and five (3%) Golden-winged Warblers that fledged independently of our activities died from apparent exposure the first or second night after fledging. Exposure mortalities occurred during exceptionally cold and usually wet nights primarily in Sandilands PF, our northernmost study site. All other mortalities were attributed to predation by mammals, hawks and snakes.

DISCUSSION

Force-fledging in response to investigator activities is widely believed to decrease reproductive success through reduced survival of fledglings, and many authors caution against it. However, little or no empirical evidence has been published in the scientific literature to evaluate this assumption. In two species of ground-nesting forest warblers (Ovenbirds and Golden-winged Warblers) in the western Great Lakes region of central North America, we found that force-fledging did not negatively influence fledgling survival. Indeed, nestlings that fledged in response to our research activities experienced survival as high as or higher than those that fledged independently of our activities. We speculate that this somewhat unexpected result is related to the condition of individual nestlings and broods, and we do not suggest that purposely forcing nestlings to fledge would positively influence fledgling survival. It is likely that a propensity or ability to fledge in response to a stimulus reflects nestling condition, with nestlings in better condition than other nestlings of similar age, even brood-mates, more likely to fledge. If the birds that force-fledged were indeed of superior condition to nestlings of similar age, it is possible that their survival would have been higher still if they had fledged later, but that hypothesis is untestable because a bird cannot be both force-fledged and allowed to fledge naturally. Unfortunately, in a separate analysis we found that differences in nestling digestive contents rendered nestling mass useless as an indicator of relative condition (H.M. Streby unpubl. data), so we could not test this hypothesis. It is also possible that force-fledged birds were negatively affected in unseen ways through longer-term energetic compensation for a short-term deficit. However, we observed no differences in daily movements or survival between force-fledged fledglings and other fledglings beyond the first week following fledging (H.M. Streby unpubl. data). Importantly, we found no evidence that nestlings that prematurely fledged experienced reduced survival, suggesting that those birds were likely to have been prepared to fledge when we banded and attached transmitters to nestlings. We suggest that broods and individual nestlings that readily fledge in response to predators or investigator activities should

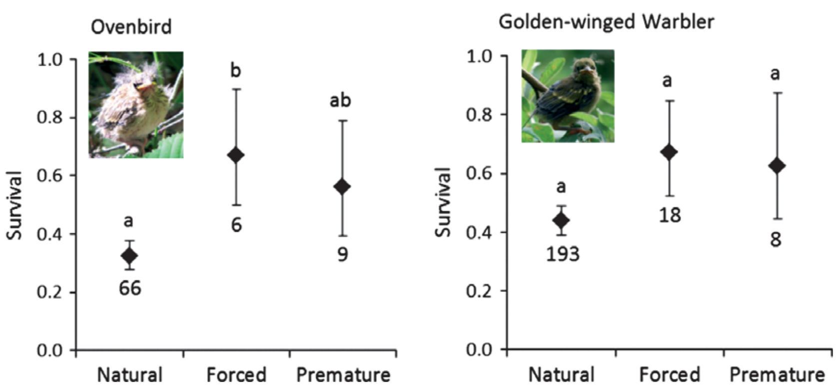

Figure 1. Survival from fledging to independence from adult care for Ovenbirds and Golden-winged Warblers that fledged from nests independent of investigator activity (natural), and those that fledged in response to investigator activity at a typical fledging age (forced) or earlier than typical fledging age (premature). Diamonds and whiskers represent means and se, respectively. Numbers and letters denote number of fledglings and significantly different groups for each species.

not be described as fledging prematurely, a term that implies fledging prior to when a fledgling is capable of surviving at typical rates.

Video surveillance of songbird nests suggests that force-fledging in response to mammalian, avian, reptilian and invertebrate predators is common in songbirds (Pietz *et al.* 2012). Lima (2009) suggested that force-fledging might be beneficial only if nestlings are sufficiently ambulatory to elude predators. Although capable of travelling > 100 m within a day of fledging (Streby & Andersen 2013a), recently fledged Ovenbirds and Golden-winged Warblers are not impressive locomotors compared with their predators. However, having one large prey item (i.e. the entire brood) become multiple separate prey items (i.e. fledglings) is likely to have some fitness benefit. The nestlings we force-fledged usually travelled < 3 m in apparently random directions from the nest and then remained silent and motionless while the adults loudly and actively distracted us, presumably as they would for any other perceived predator. Our results suggest that nestlings need only thermoregulatory, not considerable ambulatory, preparedness for force-fledging to be an adaptive behaviour.

Clearly, force-fledging prior to when nestlings are capable of surviving outside the nest (e.g. unable to thermoregulate effectively) would decrease survival due to exposure and possibly predation. However, video monitoring of nests suggests that nearly all force-fledging (whether predator- or researcher-induced) occurs after *c.* 80% of the typical nestling stage length (Ball & Bayne 2012, Pietz *et al.* 2012), similar to our observations. We speculate that force-fledging may only occur after a certain threshold (i.e. adequate condition to survive outside the nest) is reached. However, we suggest it is prudent to avoid force-fledging under circumstances that probably would compromise fledgling survival (e.g. nests high in trees, nests over water, or during inclement weather). We further caution that our results should not inspire a new assumption that force-fledging is universally harmless. However, in circumstances where research objectives require handling nestlings near fledging age, the assumption that force-fledging will always negatively influence fledgling survival is not supported by our results. For example, radiotracking fledgling songbirds is becoming increasingly common (e.g. King *et al.* 2006, Berkeley *et al.* 2007, Streby & Andersen 2013c). Attaching transmitters to nestlings too early can result in poorly fitted harnesses falling off in the nest (pers. obs.). However, waiting for birds to fledge before attaching transmitters presents additional challenges because fledglings often leave natal territories shortly after fledging, greatly reducing the probability of capture and increasing the probability of confusing unmarked broods with each other (Streby & Andersen 2013a). Furthermore, marking birds after they fledge potentially excludes fledgling mortalities that occur in the first few hours or days after fledging (Streby & Andersen 2013b). The ideal time for attaching transmitters to nestling songbirds is therefore during the 20% of the nestling stage preceding expected fledging, the period during which force-fledging some birds is likely. Our results suggest that, at least for Ovenbirds and Golden-winged Warblers, concerns about force-fledging should not be a deterrent to handling birds near the expected fledging age. In addition, if birds are inadvertently force-fledged it may be counterproductive to attempt to gather and force them back in the nest, risking disturbance to surrounding vegetation, attraction of predators to the area, injury or mortality of fledglings, and additional stress to fledglings and adults.

Force-fledging may also influence estimates of nest survival, because predation is often highest in the final days and hours of the nestling stage (Martin *et al.* 2000, Streby & Andersen 2013a) and those predation events could be precluded if young fledge early. However, video monitoring and radiotelemetry studies have demonstrated that fates of empty nests are sometimes incorrectly identified by observers anyway (Pietz *et al.* 2012, Streby & Andersen 2013a), and that estimates of productivity based solely on data from nests can be misleading regardless of assumptions about ambiguous nest fates (Streby & Andersen 2011). Our assessment of the impacts of force-fledging further supports the importance of monitoring juvenile songbird survival beyond when fledglings leave the nest. Leaving the nest is merely one occurrence during the highest mortality period for young songbirds, a most inopportune transition during which to cease data collection and make assumptions about fates of birds or the impacts of investigator activities.

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