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Short communication

# Sanitation of entire broods of dead nestlings may bias cause-specific nest failure rates

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Parent birds of many altricial species remove nestling excrement (Blair 1941), eggshells (Montevecchi 1974), foreign debris (e.g. rings on nestlings; Berger 1953), ectoparasites (Hurtrez-Bousses *et al*. 2000) and dead nestlings (Skutch 1976) from their nests; a set of behaviours collectively known as nest sanitation (Welty 1982). When sanitizing a nest of dead nestlings, parent birds typically remove a single dead nestling from a nest that contains other live nestlings (Payn 1966, Davis 1967), thus modifying slightly the contents of the nest. Observations of nest contents by field personnel are often used to infer nest fates (e.g. depredated, abandoned). For example, standard nest-monitoring protocols dictate that nests found empty and intact (i.e. nest cup and lining undisturbed) well before the anticipated fledge date are likely to have been depredated (Martin & Geupel 1993, Ralph *et al*. 1993). We provide evidence that an empty, intact nest may not always indicate a nest depredation, but instead may result from the sanitation of an entire brood of dead nestlings by parent birds following complete brood mortality (probably caused by inclement weather or starvation). Sanitation of entire broods of dead nestlings by parent birds is unreported in the literature and has implications for nest-monitoring studies that estimate cause-specific nest failure rates (Etterson *et al*. 2007).

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We observed this behaviour while monitoring breeding populations of Red-faced Warblers *Cardellina rubrifrons* and Yellow-eyed Juncos *Junco phaeonotus* in the Santa Catalina Mountains, Pima County, Arizona, USA. Red-faced Warblers and Yellow-eyed Juncos are monogamous, ground-nesting birds that breed in montane forests of the southwestern USA and Mexico (Martin & Barber 1995, Sullivan 1999, Corman & Wise-Gervais 2005). Within the Santa Catalina Mountains, both species breed concurrently (late April to early July), have similar incubation and nestling period lengths (approximately 25 days combined) and select similar nest-sites (Martin & Barber 1995, Sullivan 1999, C. Conway & C. Kirkpatrick unpubl. data). Red-faced Warblers have a modal clutch and brood size of four, whereas Yellow-eyed Juncos have a modal clutch size of four and a modal brood size of three (C. Conway & C. Kirkpatrick unpubl. data). Nest depredation accounts for > 90% of all nest failures and Gray Fox *Urocyon cinereoargenteus* (an olfactory predator) is one of the principal nest predators of both species (C. Conway & C. Kirkpatrick unpubl. data).

During the 2006 breeding season, we located and monitored 76 Red-faced Warbler and 76 Yellow-eyed Junco nests on five 16–20-ha study sites within high-elevation (2367 m to 2791 m asl) forests of the Santa Catalina Mountains using standard nest-monitoring methods (Martin & Geupel 1993). We briefly visited each nest every 2–3 days to check nest status. We recorded nest status as active if we observed (from a distance) parent birds on or in the immediate vicinity of nests and we approached nests to verify nest status and nest contents if parent birds were absent (*sensu* Martin *et al*. 2000). We assumed that a nest had been depredated when eggs or nestlings were missing (Martin & Geupel 1993, Ralph *et al*. 1993, Martin 1998). We used a protocol modified from McQuillen and Brewer (2000) to monitor continuously a subset of nine Red-faced Warbler and nine Yellow-eyed Junco nests using time-lapse video cameras equipped with infrared illumination for night-time photography (henceforth 'video cameras'; Fieldcam TLV, Fuhrman Diversified Inc., Seabrook, Texas, USA). When we checked video camera nests in the field and found that they had been depredated (or so we assumed), we continued video-taping at the nests for 24 h before dismantling the video cameras and reviewing video tapes to determine the exact cause of the nest failures.

While monitoring nests with video cameras in July 2006, we observed two instances in which parent birds sanitized nests by removing their entire brood following the apparent death of the nestlings. In the first instance, video footage showed a female Yellow-eyed Junco brooding two 1-day-old nestlings (and incubating one apparently infertile egg) during the morning of 5 July 2006 at a nest located near the summit of Mt. Lemmon, the highest point in the Santa Catalina Mountains. At 8:17 h, the brooding female sat up and began pecking vigorously at the nestlings (presumably to check if the nestlings were still alive). The


**Figure 1.** Still image from video footage taken on 5 July 2006 showing a female Yellow-eyed Junco *Junco phaeonotus* removing the second of two nestlings that died following a strong thunderstorm on 4 July 2006 in the Santa Catalina Mountains, Arizona, USA. Date and time are indicated in the upper left corner of frame.

female continued to peck at the nestlings for approximately 180 s before flying away from the nest carrying a nestling in her bill. At 8:30 h, a parent bird returned to the nest and removed the second nestling after pecking at it for approximately 25 s (Fig. 1). A field observer checked the contents of the nest at 12:15 h, found the nest with only one egg and recorded that the nest had been partially depredated. The field observer also noted that the nest cup and lining were intact. Video footage revealed that the parent birds made several visits to check the nest or to sit on the remaining egg from 8:30 h to 18:05 h, at which point the parent birds abandoned the nest.

In the second instance, video footage showed a female Red-faced Warbler brooding and feeding (on one occasion only) three 4-day-old nestlings during the morning of 6 July 2006 at a nest located in Marshall Gulch, 3 km southeast of the summit of Mt. Lemmon. This activity ended at 10:27 h when the female left the nest. A parent bird returned to the nest at 15:11 h (almost 5 h after the last visit), at which point the parent bird pecked vigorously at the nestlings for approximately 60 s. The parent bird flew away from the nest carrying what appeared to be nestlings in its bill at 15:14 h and again at 15:23 h (we observed only two trips away from the nest, but believe that the parent bird carried away all three nestlings during these two trips). Video footage revealed that the parent bird never returned to the nest and the nest remained undisturbed by nest predators until a field observer checked the contents of the nest at 12:36 h on 7 July 2006. The field observer found the nest empty and recorded that it had been depredated. The field observer also noted that the nest cup and lining were intact.

Both the Red-faced Warbler and Yellow-eyed Junco nests failed 1–2 days after a series of strong thunderstorms dropped an average of 63 mm of precipitation across our study sites between approximately 13:00 h on 4 July 2006 and 13:00 h on 6 July 2006 (Fig. 2; Mt. Lemmon and Marshall Gulch weather stations, Pima County 2006). The precipitation recorded during this 48-h period was substantial (accounting for 9% of the 681 mm average annual precipitation total; Brown 1994) and marked the beginning of the summer monsoon. Moreover, ambient temperature declined substantially during the thunderstorms: for example, ambient temperature fell from 19 °C to 12 °C at the start of the first major thunderstorm on the afternoon of 4 July 2006 (Mt. Lemmon weather station, University of Utah 2007).

Although the female Yellow-eyed Junco initially brooded her nestlings during the thunderstorm on 4 July 2006, she abandoned the nest after only 25 min when the nest became partially flooded by hail and rain (evident on video footage). We believe the Yellow-eyed Junco nestlings probably drowned or died from hypothermia shortly after the thunderstorm began because of the quantity of hail and rain that accumulated around the nest, the attendant decrease in ambient temperature, the absence of the brooding female, and the young age (1 day) of the nestlings. Moreover, the nestlings were unresponsive to subsequent feeding attempts by the male Yellow-eyed Junco immediately following the storm. Inclement weather can lead to complete brood mortality (Stewart 1972, Imanishi 2007) and young, altricial nestlings are especially vulnerable to cold because of their inability to thermoregulate (Dunn 1975).

We speculate that the Red-faced Warbler nestlings died from some combination of starvation and hypothermia. After the nestlings hatched on the afternoon of 2 July 2006, video footage showed only one parent (presumably the female) feeding and brooding nestlings, suggesting that the male died or abandoned the nest prior to the hatch date. Although the female fed and brooded the nestlings during the 48-h period of inclement weather, she took long off-bouts from the nest between thunderstorms, culminating with an off-bout of almost 5 h just before the nestlings died and the nest was sanitized. We cannot say to what extent the thunderstorms contributed to the death of the nestlings, but we believe that the inclement weather likely hastened the failure of the nest. Inclement weather can inhibit foraging by adult birds, potentially reducing their ability to survive (as suggested in Boyle 2006) and provision young (Stewart 1972, Kepler *et al.* 1996).

In general, nest sanitation is thought to be an adaptive behaviour that has evolved to limit infestations by nest parasites (Silver 1977), reduce egg-capping by stray eggshells (Montevecchi 1974, Derrickson & Warkentin 1991), provide supplemental nutrition for parent birds (e.g. ingestion of faecal sacs; Morton 1979) or reduce the potential of nest depredation (Tinbergen *et al.* 1963, Silver 1977). For example, the removal of a dead nestling from a nest following a partial brood mortality may serve to

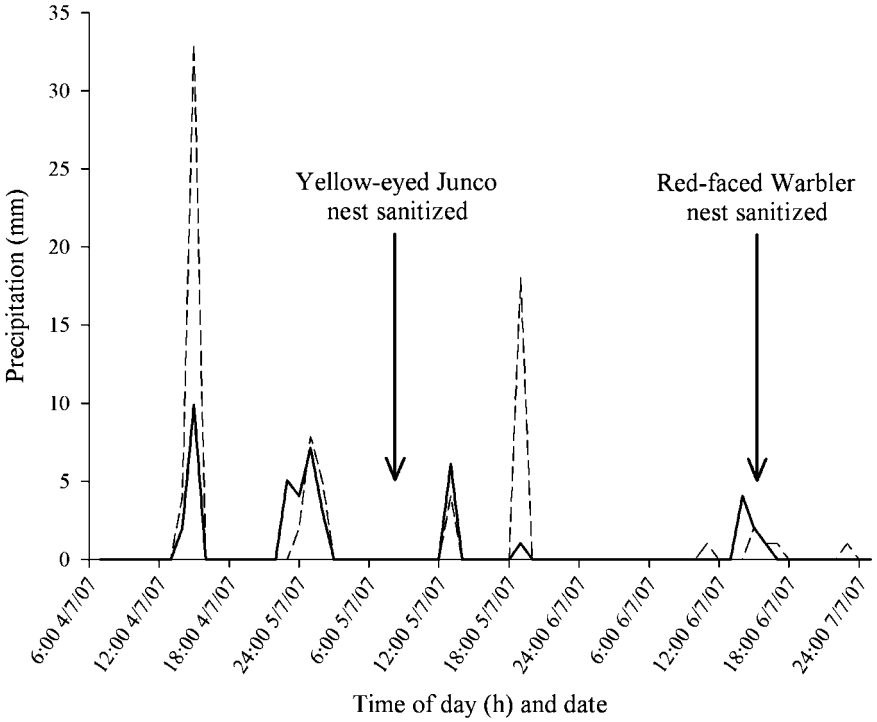


**Figure 2.** Rainfall totals (mm) taken between 6:00 h on 4 July 2006 and 24:00 h on 7 July 2006 at the Mt. Lemmon (dashed line) and Marshall Gulch (solid line) weather stations, Santa Catalina Mountains, Arizona, USA (Pima County 2006). The two arrows indicate the times and dates that parent birds were observed (on video tape) sanitizing nests of all dead nestlings at a Red-faced Warbler nest located in Marshall Gulch, and at a Yellow-eyed Junco nest located near the summit of Mt. Lemmon. Rainfall data were collected hourly at both weather stations (Pima County 2006).

reduce the risk of nest depredation by olfactory predators during the current nesting attempt. In a similar manner, parent Red-faced Warblers and Yellow-eyed Juncos observed during the current study may have removed entire broods of dead nestlings from their nests following complete brood mortalities to reduce the probability of nest depredation by olfactory predators during subsequent nesting attempts within their breeding territories.

In contrast, sanitation of entire broods of dead nestlings by parent birds may result from an innate behavioural program that is triggered by an environmental stimulus (e.g. a dead nestling) and, once started, is carried through to completion (i.e. an empty nest; Gould 1982). However, we observed three instances during 5 years of nest monitoring in which complete brood mortality following inclement weather did not result in the sanitation of dead nestlings by parent Red-faced Warblers (C. Conway & C. Kirkpatrick unpubl. data), suggesting that the behaviour varies among individuals. This variation could be based on differences in the age or experience level of breeding birds (Gould 1982) or differences in the spatial or temporal risk of nest depredation by olfactory predators. Further research is needed to examine the underlying cause(s) of sanitation of entire broods of dead nestlings by parent birds, the extent of variation in this behaviour, and the factors that predict its occurrence.

Given that complete brood mortality is a prerequisite for sanitation of entire broods of dead nestlings, we suggest that researchers pay particular attention to assigning fates to empty, intact nests during times when the risk of complete brood mortality is high. For example, complete brood mortality is more likely to occur: (1) in areas that experience bouts of inclement weather (Stewart 1972, Imanishi 2007), (2) at nests that are prone to flooding (e.g. ground nests; Shriver *et al.* 2007) and (3) when nestlings are young and susceptible to hypothermia (Dunn 1975). In addition to weather-related nest failures, complete brood mortality is more likely to occur as a result of starvation: (1) in environments where food resources are limited or highly variable (Bensch 1992), (2) when one parent is killed or abandons a nest (Duckworth 1992) and (3) in polygynous species in which males must partition their time among multiple nests (Dyrcz 1986, Johnson *et al.* 1993, but see Urano 1992).

Subsequent sanitation of entire broods of dead nestlings following complete brood mortality is likely to vary among and even within species (as evidenced by Red-faced Warblers in the current study). Therefore, researchers should

endeavour to estimate the relative frequency with which this behaviour occurs on a species-by-species basis to avoid classification errors in assigning nest fates. The probability that a researcher will witness a parent bird removing a dead nestling from a nest is remote (Mayer-Gross 1966). However, researchers can improve their odds of witnessing such events by checking nests frequently (assuming increased nest checks do not adversely affect nesting success; Etterson *et al*. 2007) or by employing video cameras at nests (as in the current study; Pierce & Pobprasert 2007) following events that increase the probability of complete brood mortality. Data collected in this manner should allow researchers to reduce bias in cause-specific nest failure rates resulting from the misclassification of nest fates. In the meantime, researchers should use caution when assigning fates to empty, intact nests and not assume that nest depredation is the sole cause of these nest failures.

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