

ORIGINAL ARTICLE

Offspring size as an index of habitat degradation

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Abstract Disturbances that shift a community away from its potential natural state may also degrade the quality of that community for some species. Having an index to measure changes in habitat quality resulting from such disturbances would be useful in assessing the impact of human activities on native fauna. We propose that average egg mass per clutch and offspring size for a population in a particular habitat may be a useful index of habitat quality, and perhaps degradation, for that population relative to the status of populations occupying other similar habitats in that region. We studied American Robins (*Turdus migratorius*) breeding along streams in three canyons on the western side of the Toiyabe Mountains of central Nevada, USA. The level of habitat degradation associated with cattle grazing and other human activities was determined *a priori* based on soil and understory vegetation characteristics. The density of adult birds and their body condition did not differ among canyons with differing habitat quality, nor did clutch size or brood size at day 8. However, nests containing larger eggs and chicks were associated with canyons assessed as having a higher quality, or lower level of degradation.

Key words Egg and chick size, Great Basin Desert, Habitat quality, Index, Livestock grazing

Larger eggs typically result in heavier nestlings with greater growth rates than the young arising from smaller eggs, for at least a short period after hatching (Williams 1994). Egg size also may influence nestling survival for both precocial (e.g., Blomqvist et al. 1997) and altricial (e.g., Bolton 1991; Smith & Bruun 1998) species, although the extent of influence depends upon circumstance. Most of the variation in egg size is among rather than within clutches, and egg size can be strongly heritable (Christians 2002). Positive correlations also are seen between environmental factors and female condition and egg size (Smith et al. 1993; Potti 1999; Styrsky et al. 2002), although female size and mass alone typically explain 20% or less of the variation in the egg size within species (Christians 2002). It is not clear that there is a relationship between egg size and fitness of the re-

sulting offspring (Williams 1994). However, if larger egg size leads to larger, faster growing chicks, then these traits could result in enhanced juvenile survival and recruitment (Tinbergen & Boerlijst 1990; Cichon & Lindén 1995; Saino et al. 1997). The role of habitat quality in determining the size and number of eggs and chicks produced has been examined for a wide range of species. Whereas studies of some species indicate no link between quality of the surrounding habitat and egg size (Smith & Bruun 1998) or chick size (Hinsley et al. 1999), many have found lower habitat quality associated with decreased offspring body mass (Lens & Dhondt 1994; Verhulst et al. 1997; Turner & McCarty 1998; Hinsley et al. 1999; Huhta et al. 1999).

One of the major sources of habitat degradation in the Great Basin of the U.S.A., particularly in the riparian areas of this region, is overgrazing by livestock (Knopf et al. 1988, Fleischner 1994; Knopf & Samson 1994; Brown & McDonald 1995). The concentrated activities of domesticated animals can change vegetative structure and species composition, alter soil structure and porosity, and modifying

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stream bank morphology (Smith 1940; Ellison 1960; Brown 1978; Kauffman & Krueger 1984; Baker & Guthery 1990; Smith et al. 1994). In addition, large stretches of riparian vegetation in this region have been destroyed or degraded by water diversions, agricultural development, mining activities, and road construction (Chaney et al. 1990; Brussard et al. 1998). The effects of these activities include reduction of natural vegetation, stream channel widening, and lowered water tables (Kauffman & Krueger 1984; Platts 1991; Fleischner 1994; Belsky & Blumenthal 1997). Consequently, the structurally diverse undisturbed native riparian flora is simplified by disturbance, which in turn modifies the native bird communities typically present (Dobkin 1994; Warkentin & Reed 1999).

Although there is recognition of the links between habitat quality and size of the young produced, to our knowledge no one has proposed that features of offspring size in a particular habitat might be a useful predictor of the quality, or extent of degradation, of one habitat relative to others in the same region. We test the hypothesis that average egg mass per clutch and offspring size are potential indices of relative habitat degradation for altricial songbirds. Our work was done in riparian forests of the Great Basin, with habitat degradation determined independently *a priori* based on soil and understory vegetation characteristics.

METHODS

1) Study area

We studied American Robins (*Turdus migratorius*) breeding along three permanent streams in the relatively narrow and steeply-walled canyons on the west slope of the Toiyabe Mountains, Lander and Nye Counties, in central Nevada, USA (39°N, 117°W) in 1995 and 1996. Study areas along streams ranged in elevation from 2050–2300 m in San Juan Creek, and 2250–2600 m in Stewart and Clear Creeks. San Juan Creek lies 24 km north of Stewart and Clear Creeks and is separated from them by several ridges reaching 2800–3000 m. Stewart and Clear Creeks lie adjacent to one another, separated by a single ridge 2700 to 3000 m high. For all three creeks, the dominant riparian vegetation on the 50–200 m wide canyon floor is quaking aspen (*Populus tremuloides*) interspersed with willow (*Salix* spp.) and water birch (*Betula occidentalis*). Away from the riparian zone are steep, rocky slopes with sparse upland forests of single leaf

pinyon (*Pinus monophylla*), Utah juniper (*Juniperus osteosperma*), and scattered patches of curl leaf mountain mahogany (*Cercocarpus ledifolius*). Primary understory shrubs include sagebrush (*Artemisia* sp.), wild rose (*Rosa woodsii*), and snowberry (*Symphoricarpos albus*). Each canyon contains grassy meadows characterized by dense cover of *Carex nebrascensis*, *C. aquatilis*, *Poa secunda*, *Juncus balticus*, or *Deschampsia cespitosa*, and extended stream banks that are used by robins for foraging and as a source of mud for nests. Length of the area sampled within each canyon was estimated using 1:50,000 topographic maps.

2) Assessing degradation

Habitat degradation was determined based on soil and understory vegetation characteristics using a ranking scheme developed by Weixelman et al. (1996). These characteristics were examined at four locations along San Juan Creek for this assessment, as well as three in both Stewart and Clear Creek canyons (D. Weixelman, D. Zamudio & K. Zamudio, U. S. Forest Service, Sparks, NV, unpubl. data). Locations were assigned an ecological status rank relative to the potential natural riparian community that would be established if successional sequences were completed without human-caused disturbances (Weixelman et al. 1996). This ecological status rank reflected high, moderate or low levels of similarity to the potential natural community. Aerial photographs were used to estimate the proportion of the study area in each canyon represented by the sample locations. To develop a quantitative value for comparing canyons, we converted these ranks for each location to a numerical score of 3, 2 or 1; a rank of 3 reflected a location with characteristics representative of the natural condition, whereas a rank of 2 indicated less similarity to the natural condition and a rank of 1 suggested limited or no similarity to natural successional patterns in the resulting community. We then calculated the average ecological status score for each canyon based on the four or three locations evaluated within each drainage.

We assessed the extent of habitat degradation in the three canyons using three additional parameters. Based on aerial photography, the percent of habitat within 100 m of each stream that contained riparian vegetation was determined, as well as the percent of riparian habitat along our study streams through which dirt roads passed or where roads defined the edge of the riparian habitat (D. Weixelman, D. Zamu-

dio & K. Zamudio, U. S. Forest Service, Sparks, NV, unpubl. data). Based on the similar topography and soil types of the three canyons, we assumed that all drainages had the same initial potential to contain riparian vegetation within the 100 m strip of land along the stream (cf. Weixelman et al. 1996). We also assumed that differences in the amount of riparian vegetation relative to other canyons were the result of different disturbance histories. Accurate grazing histories and recreational visitation rates were not available for these drainages, so dirt road cover was used as an indirect measure of road-based disturbance. Finally, we qualitatively assessed the presence or absence of severe down-cutting (streambanks with non-vegetated vertical drops ≥ 0.3 m) along significant portions of each stream.

3) Study species

The American Robin is an abundant riparian specialist in the Great Basin during the breeding season. It forages primarily on the ground, requiring a constant source of invertebrates to raise the 2–3 broods produced by each pair per year. The robin's diet and foraging ecology are relatively well studied (Sallabanks & James 1999), and nests are easily located; adults tolerate multiple nest visits (Ortega et al. 1997).

We censused adult robins and their nests in all suitable habitats along each stream. To assess relative densities of adult robins in the three canyons, from late June through early July 1996 we placed sets of 10 standard 12-m mist nets at randomly selected low, medium, and high elevation stretches in each canyon for a total of 700 mist-net hours. This timing meant that the average successful nest (based on mean clutch initiation date in each canyon) had recently fledged young. To standardize for any potential seasonal effects, all trapping events at a given elevation (i.e., low, medium, high) took place within 7 d of one another. An index of adult density was calculated as the overall capture rate per 100 net hours divided by the area of riparian vegetation in that canyon. Upon capture, adults were sexed following the criteria of Pyle et al. (1987), color banded, and their mass and tarsal length measured; age could not be reliably determined based on the criteria of Pyle et al. (1987). We tested for differences in overall body size among canyons for each sex using a Kruskal–Wallis one-way analysis of variance (ANOVA). This test was based on examining PC-1 scores from a principal components analysis (PCA) of tarsus and mass (Free-

man & Jackson 1990). The adults captured were not necessarily the birds present at nests where reproductive success variables were measured, so we could not correlate adult condition with success of a particular nesting attempt. We assumed, however, that the condition of trapped birds represented the average condition for adults, including breeding birds, in each canyon.

Nest searching was initiated on 1 June 1995 and 1 May 1996 with each canyon searched every 4–5 d through the middle of July for both years. Because we could not distinguish between first and later broods, data for all nests were pooled for these analyses. The difference between years in the start of nest searching constituted a systematic bias that would not alter comparisons between canyons across years.

Nests found before or during egg laying were revisited every 3 d until clutch completion so that clutch initiation dates, final clutch sizes, and estimated hatch dates could be determined. Nests located after clutch completion were checked every 3 d to determine hatch date. We estimated clutch initiation dates for nests found after clutch completion by subtracting the average incubation time of 13 d (Sallabanks & James 1999) from the date of hatch. When nests were discovered after hatching, we estimated clutch initiation date based on an average incubation time of 13 d in combination with chick age determined from an ageing key developed using known-age chicks (day 0 being when the first egg hatched; Warkentin et al. 2003). We compared initial clutch size and brood size at day 8 among canyons, once including all nests, and once including only those nests that had one or more chicks at day 8, using a Kruskal–Wallis ANOVA.

For all nests found during incubation with at least 3 eggs, we measured the maximum length (L) and breadth (B) of each egg to the nearest 0.1 mm using digital calipers. We converted these values to fresh egg mass (W) to assess differences in the amount of resources invested in eggs by females in different canyon types. Fresh egg mass was calculated as $W = K_w LB^2$, where K_w is a shape-specific mass coefficient reported for American Robin eggs by Hoyt (1979). Mean egg mass, as well as mass of the largest and smallest egg in each clutch were compared among canyons using Kruskal–Wallis ANOVAs.

Robin eggs hatch asynchronously with broods of three typically hatching over two days and broods of four or five hatching over three days (Slagsvold 1997). As a result, there are marked differences in

body size among individuals in a nest at a given point in the nestling phase. Therefore, we based our assessment of body size for chicks in a nest on morphological measurements from the largest chick at day 8 of the nestling phase in each nest. Interestingly, the largest individual on day 8 was not always the first to hatch because sometimes a chick's growth was retarded, apparently from extensive black fly bites. We measured mass, tarsus length, total head length, and bill length to the nearest 0.1 mm using digital calipers. These measurements were combined using PCA to develop a single measure of body size that could be used to compare chicks among canyons using a Kruskal–Wallis ANOVA. Although American Robins fledge between day 14 and 16 (Sallabanks and James 1988), we avoided handling nestlings older than 8 days to prevent premature fledging. We defined successful nests as those having at least one chick alive on day 8.

4) Statistical analyses

Clutch initiation date and fledging success data were collected and calculated for all nests encountered regardless of nestling age. Nests used in egg and chick size comparisons represent a subset of the total number of nests sampled as not all nests found were at the same stage of the breeding cycle or could necessarily be visited on day 8 to collect morphological data.

This is an exploratory assessment (*sensu* Steidl et al. 1997) of the predictive power of offspring size relative to habitat degradation, thus accepting $P \leq 0.10$ as statistically significant is appropriate. Where Kruskal–Wallis ANOVA indicated a significant difference among canyons for a particular variable, we conducted a post-hoc examination of the main effects. For the post-hoc test, we rank-transformed the data and then repeated the ANOVA (*cf.* Conover & Iman 1981) using Fisher's LSD to make post-hoc multiple comparisons; for these post-hoc tests we used an alpha level of 0.1. We conducted all statistical analyses using SAS version 8.12 (SAS Institute Inc. 2001).

RESULTS

San Juan Creek canyon was the most heavily degraded of the three canyons (Table 1). This canyon had the lowest area of riparian vegetation (varying from 4 to 28 m wide), in combination with the highest percentage of riparian habitat covered or bordered

by roads, the presence of severe down-cutting along significant proportions of the stream, and the lowest average ecological status score. Based on the same measures, Stewart (with a 15 to 45 m wide riparian zone) and Clear (with a 50-m wide riparian zone at all three locations examined) Creek canyons are similar in their degree of degradation, but Clear Creek may be relatively less degraded based on the higher proportion of riparian vegetation present and its higher average ecological status score (Table 1).

Data from mist-netting indicated that the density of adult robins was similar among canyons (Table 2). For adults captured, female and male size based on the PC-1 score, which explained 66.2% of the variance, did not differ among canyons when examined with a Kruskal–Wallis one-way ANOVA.

We found 90 active American Robin nests during two summers in the three canyons, of which 77 had known outcomes with eggs and/or chicks produced. There was a significant difference among canyons in clutch initiation date with nests in San Juan Creek canyon started on average 5.5 days before those in Stewart and 14.8 days before those in Clear (Table 2). Post-hoc testing suggested that nests in Clear Creek canyon were significantly later than those in the other two canyons which, in turn, did not differ from each other. The overall relationship probably reflected the significant correlation between clutch initiation date and nest elevation ($F_{1,66} = 5.25$, $P = 0.025$, $r^2 = 0.06$) across all three canyons. But since none of our parameters of interest (mean egg mass, clutch size, and

Table 1. Study site dimensions and characterization of degradation for riparian habitat in three canyons of the Toiyabe Mountain Range, Nevada. Criteria for percent habitat within 100 m of each stream that contains riparian vegetation, percent riparian area covered or bordered by roads, presence/absence of streambank down-cutting, and the ecological status score all suggest that relative degradation is least for Clear Creek and most for San Juan Creek canyons.

	Canyon		
	San Juan	Stewart	Clear
Length (m)	3505	4451	2713
Area of riparian vegetation (m ²)	84,120	137,981	135,650
Riparian area (%)	24	31	50
Riparian area bordered by road (%)	54	28	35
Severe downcutting	Present	Absent	Absent
Ecological status score	1.68	2.00	2.10

Table 2. Productivity and morphometric features of an American Robin population breeding in the riparian habitat of three canyons in the Toiyabe Mountain Range, Nevada. Values presented are mean \pm SE(n) along with statistics from Kruskal–Wallis analyses; those with different superscripted letters are significantly different from each other.

	San Juan	Stewart	Clear	χ^2	P
Adult					
Density (per 100 net-hours per km ²)	0.10	0.06	0.07		
Female PC-1	0.20 \pm 0.14 (6)	-0.26 \pm 0.36 (8)	0.16 \pm 0.42 (9)	1.26	0.53
Male PC-1	0.23 \pm 0.44 (6)	-0.36 \pm 0.32 (9)	0.09 \pm 0.28 (13)	0.67	0.71
Clutch					
Mean initiation date	May 22 \pm 2 (27) ^B	May 27 \pm 4 (26) ^B	June 5 \pm 4 (18) ^A	5.96	0.05
Initial size	3.8 \pm 0.2 (17)	3.5 \pm 0.1 (17)	3.6 \pm 0.1 (14)	1.32	0.51
Brood size at day 8	2.5 \pm 0.3 (27)	1.9 \pm 0.3 (28)	1.7 \pm 0.4 (17)	2.51	0.28
Brood size at day 8 (successful only)	3.2 \pm 0.2 (21)	3.0 \pm 0.2 (18)	3.3 \pm 0.2 (9)	0.48	0.78
Eggs					
Mean egg mass (g)	6.6 \pm 0.1 (13) ^B	6.9 \pm 0.2 (6) ^{AB}	7.2 \pm 0.1 (10) ^A	5.37	0.06
Smallest egg mass (g)	6.5 \pm 0.1 (13)	6.6 \pm 0.2 (6)	6.9 \pm 0.2 (10)	2.32	0.31
Largest egg mass (g)	6.9 \pm 0.1 (13) ^B	7.3 \pm 0.2 (6) ^{AB}	7.4 \pm 0.1 (10) ^A	5.17	0.07
Chicks					
PC-1 (largest chick)	-0.39 \pm 0.21 (12) ^B	0.23 \pm 0.39 (9) ^A	0.37 \pm 0.39 (7) ^A	4.76	0.09

chick size at day 8) were correlated with clutch initiation date ($F_{1,27}=2.68$, $P=0.11$, $r^2=0.09$; $F_{1,59}=0.41$, $P=0.52$, $r^2=0.007$; and $F_{1,24}=1.24$, $P=0.27$, $r^2=0.05$; respectively), we assumed that the effects we report on egg and chick size were not due to differences in elevation (as it affected clutch initiation date) among canyons. In addition, most research (e.g., Hochachka 1990) suggests that earlier hatching chicks are larger than those hatching later in the season. This is contrary to the trends that we report below.

Data on clutch and brood sizes suggested minimal differences among canyons in habitat quality. Initial clutch sizes, as well as brood size at day 8 for all nests and brood size at day 8 for successful nests only, did not differ significantly among canyons (Table 2). Partial-brood loss rates did not differ among canyons (Table 3; Fisher Exact Test, $P=0.66$), and likewise whole-brood loss rates did not differ among canyons (Table 3; Fisher Exact Test, $P=0.34$).

In general, eggs and chicks from nests in San Juan Creek canyon, the most degraded canyon, were smaller than those in Stewart Creek canyon, which in turn were smaller (but not significantly so) than those in Clear Creek canyon, the least degraded of the three (Table 2). Mean egg mass per clutch was 8% greater in Clear Creek canyon than those in San Juan Creek canyon and mean egg mass for Stewart Creek canyon was intermediate. Although egg mass of the smallest

Table 3. Nest outcomes for a population of American Robins breeding in the riparian habitat of three canyons in the Toiyabe Mountain Range, Nevada.

	San Juan	Stewart	Clear
Total number monitored	29	31	17
Outcome			
Failed	8	13	8
At least 1 young at day 8	21	18	9
Known partial brood loss	3	5	1
Brood size at day 8 equaled number of eggs laid	8	3	5

egg in the clutch did not differ among canyons, the largest egg in the clutch followed the same pattern as reported above for mean egg mass, with largest eggs from Clear being 7% heavier than those in San Juan (Table 2). We did not have morphometric data on specific individuals because we were not able to match eggs (i.e., egg mass) with individual nestlings, nor did we know hatching order of the young. We combined data for the four morphometric measures taken from the largest chick present in the nest at day 8 to create a PC-1 score, which explained 72% of the variance. This statistic indicated that nests in Clear Creek and Stewart canyons had the largest young and San Juan Creek canyon had significantly smaller young (Table 2).

DISCUSSION

Anthropogenic disturbances that shift a community away from its potential natural state may also degrade the quality of that community for some species. Having an index to measure changes in habitat quality resulting from such disturbances would be useful in assessing the impact of human activities on native fauna. Fluctuating asymmetry has been proposed as an index of habitat degradation based on developmental responses by individuals inhabiting a particular community (e.g., Badyaev et al. 2000; Leung et al. 2000; Lens et al. 2002; Zakharov 2003). These analyses of American Robins were complicated by limited sample size, a qualitative rather than quantitative assessment of habitat degradation, and differences amongst canyons in elevation. However, our results suggest a tendency for mean egg mass and chick size to vary with the extent of habitat degradation and thus such measures may be a useful index of habitat quality or degradation across suitable habitats within a region.

For passerines that depend on the daily accumulation of energy reserves to produce eggs (Perrins 1996), decreased availability or quality of food may cause females to allocate fewer resources to egg production. Reduced habitat quality could also be due to an increase in species that use disturbed areas, such as some competitors or predators (Paton 1994). In lower quality habitats, this could result in the production of smaller clutches and fewer young fledged (Cowie & Hinsley 1987) or lower body-mass chicks (Lens & Dhondt 1994; Verhulst et al. 1997; Hinsley et al. 1999). Our data suggest that American Robins did not alter the size of their clutch, but rather allocated less energy to each egg. In the most degraded habitat (San Juan Creek canyon) egg mass was on average 8% lower than for robin eggs from nests in the least degraded habitat (Clear Creek canyon). This difference in mean egg mass is similar to the maximum increase in egg size attributable to dietary supplements (Christians 2002).

Condition of breeding females (an index of mass relative to body size) and egg mass have been shown to be significantly correlated in a number of species (Slagsvold & Lifjeld 1989; Smith et al. 1993; Potti 1999; Styrsky et al. 2002). However, since female mass and size typically explain 20% or less of the variation in the egg size within species (Christians 2002), it appears to be the ability to translate environmental resources into egg mass that is important and

not necessarily overall body size. We trapped adults later in the season when females may have lost mass accumulated during egg laying, but we detected no difference in female size among canyons.

Some studies suggest that the effect of egg mass on chick size disappears with nestling age and is gone by the time of fledging (Magrath 1992; Smith & Bruun 1998). Smith and Bruun (1998) also found that neither egg nor nestling masses were related to the availability of high quality foraging habitat for starlings, but that this habitat variable did influence nestling survival late in the nestling period. This contrasts with our results, which indicate that there were no differences among canyons in initial clutch sizes or brood sizes at day 8. Smith and Bruun (1998) also suggested that availability of high quality habitat may only influence the translation of large egg size into large nestling size when habitat availability is limited, although egg size did not vary with availability of high quality foraging habitat in their study. Bize et al. (2002) proposed that rearing conditions, reflected by the size of eggs laid by the care-giving parent (real or foster), were more important than initial egg mass in predicting survival. The latter result contrasts with the findings of Schifferli (1973) but concurs with Reed et al. (1999) who found that survival and growth of nestlings were largely influenced by factors other than egg size.

Although measurable morphometric differences may disappear in the nestlings of some species by the time they fledge, it appears that the impact of this difference during rearing may influence the ability of an individual to obtain a high quality nesting site in the future. Verhulst et al. (1997) found that Great Tits (*Parus major*) that were relatively heavier as nestlings bred in better quality habitat as adults, and other studies suggest that these individuals will have better reproductive performance than individuals who were lighter as nestlings (Green & Cockburn 2001; Perrins & McCleery 2001; Styrsky et al. 2002).

In arid ecosystems, the presence of roads and overgrazing can adversely affect the quality of riparian habitat for some members of the biological community and lead to either population decline or loss (Fleischner 1994; Trombulak & Frissell 2000). Based on population density measures, studies of American Robins suggest that this species may actually benefit from moderate levels of habitat degradation (Page et al. 1978; Crouch 1982; Mosconi & Hutto 1982; Sedgwick & Knopf 1987; Schulz & Leininger 1991; Warkentin & Reed 1999), but examination of fitness

components in any habitat are lacking. While intensive grazing can simplify vegetation diversity and consequently cause decreased diversity of associated phytophagous insects (Lawton & Schroder 1977), moderate grazing levels may lead to enhanced foraging opportunities for robins and increased habitat quality through providing a more diverse vegetative community (Milchunas et al. 1988; Grime 1990; Collins et al. 1998) and greater diversity among those same insects groups (Eijsackers 1983; Morris 1990; Tschardtke & Greiler 1995; Oates 1995; Kruess & Tschardtke 2002). Although no canyon-level records of grazing activity are available for our study sites, we would argue that the physical features and vegetation remaining indicate that grazing pressure had been very intensive in San Juan Creek canyon. There was a low level of similarity to the potential natural community as a consequence of both cattle grazing and high levels of human use for recreational activities which together led to the lowering of habitat quality. Consequently, we propose that the invertebrate community that forms the vast majority of the diet during the breeding season for robins in this area (see Sallabanks & James 1999) would be adversely affected by grazing and human recreation resulting in a reduced invertebrate fauna and less food available to invest the resources in eggs by female robins. This degradation was reflected in decreased quality of the young robins produced in this canyon.

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