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MATING AND BREEDING SUCCESS DECLINE WITH ELEVATION FOR THE PACIFIC WREN (*TROGLODYTES PACIFICUS*) IN COASTAL MOUNTAIN FORESTS

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ABSTRACT.—We studied the population ecology of Pacific Wrens (*Troglodytes pacificus*) in 2003 and 2004 breeding across elevations from 100 to 1,300 m in coastal mountain forests in southwestern British Columbia, Canada to examine if this species is adapted to upper montane and subalpine habitats. We found fewer territories at high elevation, a higher proportion of unmated males, fewer nests per mated male, and no returns of banded adults or juveniles. The breeding season was 61% shorter (31 vs. 79 days), and mass of nestlings (at 11–12 days of age) and nest survival were lower at high elevation compared to lower elevation sites. Clutch size, incubation and nestling periods, parental provisioning rates of nestlings, and adult morphology did not vary with elevation. Annual fecundity measures declined with increasing elevation with no apparent compensatory increases in other vital rates such as survival of adults or offspring. *Received 27 October 2011. Accepted 23 December 2011.*

The Pacific Wren (*Troglodytes pacificus*), a small migratory songbird that breeds in coastal coniferous forests of western North America, was recently described as a species distinct from the Winter Wren (*T. hiemalis*) in the rest of North America and the Eurasian Wren (*T. troglodytes*) in Europe (Wesolowski 1983, Toews and Irwin 2008, Chesser et al. 2010). Pacific Wrens are common birds of northern temperate coniferous and mixed forests of North America, but there are few studies of their breeding ecology and nesting success (McLachlin 1983, Van Horne and Bader 1990, Waterhouse 1998, De Santo et al. 2003). The Pacific Wren breeds across an elevation gradient from sea level to upper montane and subalpine habitats along the west coast of North America (Toews and Irwin 2008).

High mountain areas are characterized by variable weather, cold temperatures, and short breeding seasons (Martin 2001). At least 90 bird species breed across wide elevation gradients, some of which range from sea level to alpine habitats, but their ecology, behavior, and life history at upper elevation limits are poorly understood. Short breeding seasons at high elevations translated into lower annual fecundity for the few species studied, particularly when the ability to initiate nesting was influenced by snowmelt phenology (Martin and Wiebe 2004, Martin et al. 2009, Wilson and Martin 2010). Birds breeding at high elevations appear to compensate for reduced annual fecundity by increasing their per capita parental care, thus improving juvenile survival (Badyaev and Ghalamor 2001). Body size of adults and egg size both increase with increasing elevation (Bears et al. 2008, Zeng and Lu 2009, Lu et al. 2010). Several songbird species trade reduced annual fecundity for increased survival of both adults and young in high elevation populations (Bears et al. 2009, Martin et al. 2009, Camfield et al. 2010). These studies found intra-specific differences with elevation as high elevation populations shifted to a ‘slower’ life history with a longer life span, fewer offspring per breeding season, but greater investment in parental care. The length of the breeding season sharply decreases with increasing elevation due to later snow melt and shorter vegetative growth seasons, and birds increase their per capita parental investment. Birds at higher elevations are larger, heavier, and have higher survival (Bears et al. 2009, Martin et al. 2009, Camfield et al. 2010).

We investigated variation in the breeding ecology of the Pacific Wren along an altitudinal gradient from 100 to 1,300 m. We predicted that as elevation increased: (1) breeding season duration, the number of broods, and/or clutch size would decrease; (2) duration of incubation and nestling periods would increase; (3) per capita parental care of nestlings and offspring mass at fledging would increase; (4) birds would have higher survival; and (5) mating status would not

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differ. We expected Pacific Wrens breeding at high elevation to show a shift to a slower lifestyle with lower annual fecundity and higher survival.

METHODS

Study Species.—Pacific Wrens breed across extensive elevation gradients in western North America from the Alaskan Pacific Coast to central California and inland to Alberta, western Montana, and central Idaho (Chesser et al. 2010). They are typically associated with conifer forests, but will nest in mixed forests, on cliff faces, and in riparian habitats. Pacific Wrens use a range of types of nest sites and styles of nest construction. They are often cavity nesters, excavating holes in the root masses of upturned trees or in decaying trees or downed logs, but will also construct non-cavity nests in tree branches or riparian vegetation (Waterhouse et al. 2002). Males arrive early in breeding areas to establish territories and begin constructing multiple nests with females arriving shortly after to select a nest from the newly constructed or older nests present on the territory. Females typically lay one egg/day and complete clutches of five to seven eggs. Only females incubate eggs which hatch 14–16 days after onset of incubation. Males and females provision nestlings that usually remain in the nest 15–19 days before fledging. Pacific Wrens may raise two broods per season (Hejl et al. 2002). No blood parasites were found in adult or nestling Pacific Wrens at any elevation in coastal montane coniferous forests in British Columbia (Topp et al. 2007).

Study Area and Field Methods.—This study was conducted over two breeding seasons, May to August, 2003–2004 at Mount Seymour Provincial Park in the coastal mountain range of southern British Columbia, Canada ~15 km NE of Vancouver (49° 23′ N, 122° 56′ W). The study area encompassed two biogeoclimatic zones with low elevation sites (100–500 m) within the Coastal Western Hemlock (*Tsuga heterophylla*) zone, and high elevation sites (750–1,300 m) within the subalpine Mountain Hemlock (*T. mertensiana*) zone. We also collected field data at mid elevation (550–700 m) for several variables. The Coastal Western Hemlock zone has a mean annual temperature of ~08 °C and, in summer, temperatures are typically >10 °C (Pojar et al. 1991). The mean annual temperature for the Mountain Hemlock zone is ~0 °C with temperatures >10 °C only from mid-June through August.

We searched for, captured, and color-banded adults and juveniles during 2003–2004 and monitored active nests (nests that contained 1 or more eggs or nestlings) and potential nests (nests from previous years in good condition, nests under construction, or recently constructed nests as indicated by the presence or addition of new nest materials) along an elevation gradient (100–1,300 m). We located Pacific Wren pairs and nests using a combination of behavioral cues and intensive searching of potential nest sites. Males were captured and banded at or near nest sites using mist nets and song playbacks, and most females were captured directly off the nest during incubation using a modified butterfly net in the dim light just before dawn (mist-netting attached to a round hoop on a pole). Nestlings reach near fledging mass at 10 days of age (McLachlin 1983) and we banded most at 11–12 days of age.

Search efforts for pairs and nests in 2003 were allocated approximately evenly across elevations with time and personnel divided between sites. We focused our efforts in 2004 only on high (750–1,300 m) and low (100–500 m) elevation nests to ensure that we obtained a sufficient sample size at these altitudes. Nests were discovered during construction, laying, incubation, and nestling stages. Territories were delineated based on presence of singing males, video recordings at the nest, and on mapped locations of active and potential nest sites. Locations of color-banded males were tracked throughout the breeding season using song playbacks to assign males to territories.

Nests were visited about every 3 days to record nest status and fate. Clutch size and nestling number were ascertained with visual counts using dental mirrors and flashlights. Temperature loggers (HOBO Pro Series, Number H08-031-08, Onset Computer, Pocaset, MA, USA) were placed in nests during the incubation period with temperatures recorded at 1-min intervals to establish nest attendance patterns. This allowed us to obtain precise estimates of the time of nesting failure. Video cameras were placed 5 to 10 m from nests during the nestling period and focused on the nest entrance to record parental provisioning and brooding time behavior. All parental activity near nests within 2-hr video sessions was recorded and later transcribed by viewing video tapes to summarize the number of provisioning trips/adult/hr.

TABLE 1. Number of territories, mating status, nesting success, and survival of Pacific Wrens in relation to elevation on Mount Seymour, British Columbia, Canada.

	Low elevation (100–390 m)		High elevation (750–1,270 m)	
	2003	2004	2003	2004
A. Territories and mating status				
Number of territories	21	18	10	11
Number of unmated territorial males	0	0	3	9
Number of banded males	15	15	7	5
Average total nests/male	2.4	4.0	1.3	2.6
Percent successful nests/male	25	24	0	0
B. Annual local survival				
Adults				
Number banded	28		19	
Number returning the following year	9		0	
Juveniles				
Number banded	50		6	
Number returning the following year	1		0	

We estimated the date-of-first-egg-laid by backdating for nests discovered after onset of incubation and, where hatching and/or fledging events were observed, using average periods of 15 and 17 days for incubation and nestling periods, respectively (Hejl et al. 2002).

Data Analysis.—We used R Version 2.4.0 (R Development Core Team 2006) for all statistical analyses. Clutch initiation dates were standardized between years by subtracting the yearly median. Clutch sizes were not normally distributed and we used a generalized linear model with a Poisson distribution to analyze the response of clutch size to elevation, year, and clutch initiation date. Linear models were used to evaluate the response of clutch initiation (date-of-first-egg-laid), provisioning rates, and incubation and nestling periods to elevation. Log and square-root transformations improved model fit for clutch initiation and nestling period models, respectively. We calculated daily nest survival rates using the logistic exposure method (Shaffer 2004). ANOVA was used to test for differences in morphology and condition (wing chord, tarsus, body mass) of adults and pre-fledging nestling mass among three elevation categories (high, middle, and low elevations) and sex (adults only). Alpha was set at 0.05 and means are reported ± SE.

RESULTS

We located 22 and 24 active nests (containing eggs or nestlings), 73 and 72 potential nests (empty nests constructed and/or maintained and attended by a territorial male) and one and three recently failed nests during the 2003 and 2004 breeding seasons, respectively. Active nests were distributed over an elevation range from 102 to 1,088 m. We did not find active nests above 1,100 m, but did locate one potential nest at 1,270 m and territorial males above 1,200 m in both years. We captured the majority of adults and nestlings at active nests in 2003 and 2004. We found fewer territories in both years, and fewer males successfully obtained one or more mates at higher elevation sites (Table 1). Our sample of banded males at low elevation had more nests (including both active and potential nests) and a higher proportion of their nests were successful compared to high elevation (Table 1).

Clutch Initiation and Clutch Size.—Clutches were initiated over a span of 79 days (40 nests) at low elevation, and over 31 days (6 nests) at high elevation. There was a tendency for later clutch initiation at high elevations, but clutch initiation dates did not differ between elevations ($F_{1,42}$ = 3.26, P = 0.08). Nests at low elevations had two peak clutch initiation periods, whereas nests at high elevation had only one peak at a similar time as the second peak period at low elevation (Fig. 1A).

Mean clutch size (including first and re-nest attempts and second broods) was 5.5 ± 0.10 (n = 40) and did not vary with elevation ($Dev\ Resid_{1,36}$ = 0.15, P = 0.70), clutch initiation dates ($Dev\ Resid_{1,35}$ = 0.411, P = 0.52), or with year ($Dev\ Resid_{1,34}$ = 0.01, P = 0.93; Fig 1B). Fledglings produced per eggs laid declined from an average of 0.5 at 200–400 m to 0 above 600 m. It was not

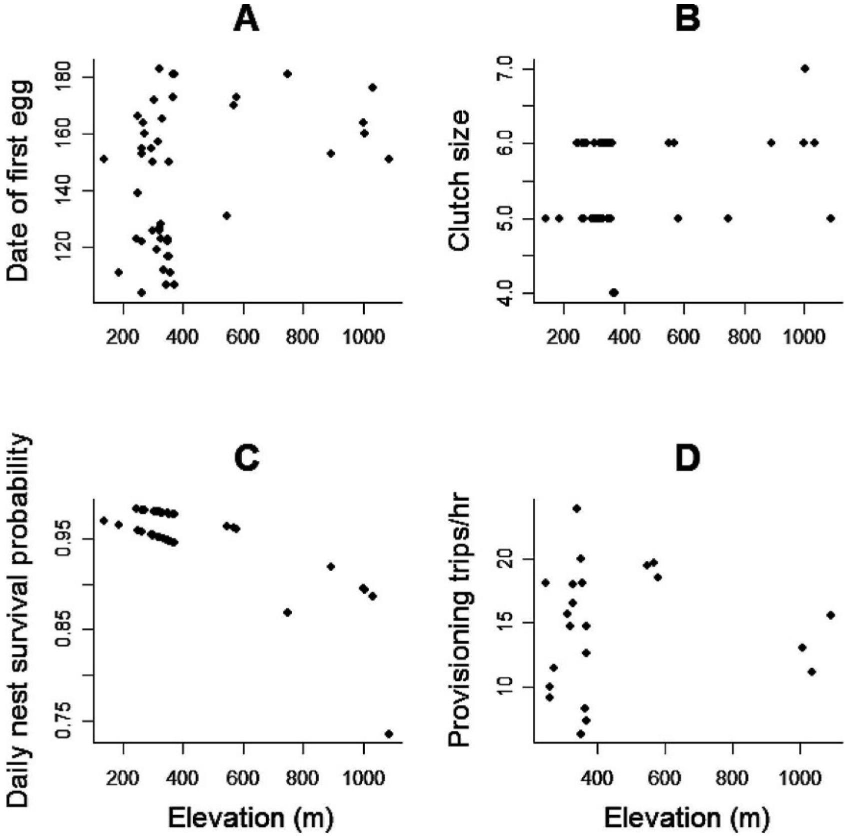

FIG. 1. Breeding parameters of Pacific Wrens nesting along an elevation gradient (100–1,100 m) on Mount Seymour, British Columbia, Canada, 2003–2004. A. Date-of-first egg (Julian date, day 1 = 1 Jan) for all nesting attempts. B. Clutch size (all nesting attempts). C. Daily nest survival probability. D. Nestling feeding rates (number of provisioning trips by adults/hr).

possible to produce a good model for these fecundity data because of our small sample; but the general relationship was non-linear and resembled a threshold with no change up to 400 m and then a decline to zero productivity.

Nest Survival.—The mean daily nest survival across elevations was 0.960 ± 0.018 (*n* = 46 nests) and ranged from 0.735 to 0.983. Daily nest survival did not vary between years ($P = 0.07$, full model: ($Dev\ Resid_{2,43} = 10.06$)) and generally decreased with elevation ($P = 0.01$; Fig 1C).

All six of our active high elevation nests failed, one during incubation, and five during the nestling stage. We encountered two families with fledglings and five hatch-year individuals at our high elevation site in 2003. Six hatch year birds were observed ‘prospecting’ in high elevation habitats (i.e., singing a recognizably juvenile male song) at different locations and times in the autumn period. None of these hatch-year birds was associated with our high elevation nests, and none returned to breed the following year.

Offspring Development Periods and Provisioning Rates.—Incubation (14.75 ± 0.33 days, *n* = 12 nests) and nestling periods (17.75 ± 0.41 days, *n* = 16 nests) did not vary with elevation ($F_{1,10} = 2.88$, $P = 0.12$; $F_{1,14} = 0.17$, $P = 0.69$, respectively). Provisioning rates (number of trips by adults/hr) did not differ with elevation ($F_{1,20} = 0.009$, $P = 0.92$; Fig. 1D); however, mass of nestlings near fledging (11–12 days after hatching) varied with elevation ($F_{2,45} = 3.36$, $P = 0.04$, Table 2). Nestling mass was similar between low and mid elevations ($F_{1,39} = 0.12$, $P = 0.73$), but nestlings reared at high elevation were significantly lighter than those at low and middle elevations pooled ($F_{1,46} = 6.74$, $P = 0.013$).

TABLE 2. Mass, wing chord, and tarsus of adult Pacific Wrens (breeding males and females) and nestlings (at 11–12 days of age) across three elevations on Mount Seymour, British Columbia, Canada. Means ± SE, sample sizes in brackets.

Elevation	Male	Female	Nestling
A. Mass			
Low	9.35 ± 0.12 (32)	8.92 ± 0.17 (21)	8.89 ± 0.20 (30)
Middle	8.96 ± 0.14 (7)	8.06 ± 0.06 (4)	9.01 ± 0.14 (11)
High	9.29 ± 0.12 (18)	9.03 ± 0.18 (10)	7.89 ± 0.37 (7)
B. Wing chord			
Low	48.30 ± 0.18 (33)	45.40 ± 0.31 (21)	
Middle	48.86 ± 0.34 (7)	45.50 ± 0.91 (4)	
High	47.58 ± 0.15 (17)	46.25 ± 0.22 (10)	
C. Tarsus			
Low	20.36 ± 0.17 (33)	19.77 ± 0.15 (21)	
Middle	20.33 ± 0.17 (7)	20.09 ± 0.36 (4)	
High	20.41 ± 0.14 (18)	20.02 ± 0.08 (10)	

Adult Morphology and Mass.—We observed few morphological differences among adult wrens breeding across elevations (Table 2). Wing chord and tarsus were longer for males than females (wing: $F_{1,88} = 101.26$, $P < 0.001$; tarsus ($F_{1,89} = 8.95$, $P = 0.00$), but neither trait varied with elevation (wing: $F_{2,88} = 0.68$, $P = 0.50$; tarsus: $F_{2,89} = 0.32$, $P = 0.70$). Adult mass varied with both sex of adult and elevation with males being heavier than females ($F_{1,88} = 9.99$, $P = 0.00$); wrens at middle elevations were lighter than those at high or low elevations ($F_{2,88} = 3.65$, $P = 0.03$). Adult mass (males and females pooled) was similar between low and high elevation (low: 9.19 ± 0.10 g, $n = 53$; high: 9.18 ± 0.10 g, $n = 28$), but birds at middle elevations were lighter, especially the four females in our sample (8.64 ± 0.16 g, $n = 11$; Table 2).

Local Adult and Juvenile Annual Survival.—Nine of 28 (33.3%) adults and one of 50 (2%) nestlings banded at low elevation in 2003, returned in 2004, respectively. None of the 19 adults and six juveniles banded at high elevation in 2003 was re-observed in 2004 (Table 1B).

DISCUSSION

Pacific and Winter wrens are reported breeding from sea level to >3,700 m (Heijl et al. 2002), but we found Pacific Wrens on our coastal mountain sites in British Columbia, had lower indices of mating status, fecundity, nestling condition, local survival, and natal and breeding philopatry at high elevations. We found no differences with elevation in clutch size, offspring development times, or per capita parental provisioning of nestlings. Thus, we found no evidence for changes in breeding ecology of Pacific Wrens with elevation and no support for our hypothesis of a shift to a 'slower' life history with increasing elevation. This contrasts to several recent studies of songbirds breeding across elevation gradients in western North America such as Dark-eyed Junco (*Junco hyemalis*), Savannah Sparrow (*Passerculus sandwichensis*), and Horned Lark (*Eremophila alpestris articola*) (Bears et al. 2009, Martin et al. 2009, Camfield et al. 2010).

The avian breeding season at high elevation can be about 60% shorter than at lower elevations. Dark-eyed Juncos breeding at 2,000 m in Jasper National Park, Alberta had a 59% reduction in seasonal duration of clutch initiation compared to juncos at 1,000 m in the same area (40 vs. 97 days; Bears et al. 2009). An alpine population of Horned Larks initiated clutches over an average period of 38.5 days, a 59% shorter duration than the 94-day clutch initiation period for a low elevation population (Camfield et al. 2010). Juncos and alpine populations of larks and Savannah Sparrows all had normal or high survival of eggs, hatchlings, and fledglings (Martin et al. 2009). The clutch initiation period for Pacific Wrens breeding at high elevation was 61% shorter than for wrens breeding at lower elevation on the same mountain; thus, there was only sufficient time to produce one brood/season at high elevation. The high elevation territories still had deep snow present with some females not yet, or only just arriving, at the same time that pairs at low elevation were fledging their first broods.

Pacific Wrens produced fewer offspring with lower mass at high elevation compared to lower elevation, in contrast to fecundity patterns observed for Dark-eyed Juncos (Bears et al. 2008, 2009), Savannah Sparrows (Martin et al. 2009), and Horned Larks (Camfield et al. 2010). Pacific Wrens did not adjust their per capita provisioning of nestlings with increased elevation to compensate for the more rigorous conditions as observed for high elevation finches and tits in Eurasia (Badyaev 1997, Lee et al. 2011). Early developmental and offspring growth patterns did not vary with elevation, and it appears that high elevation habitats are peripheral or sub-optimal breeding habitats for the Pacific Wren.

Species that are well adapted to high elevation habitats exhibit increased survival to offset reduced annual fecundity. Horned Larks breeding at 1,500–1,850 m had about 18% higher annual survival compared to birds breeding at a lower elevation and latitude (Camfield et al. 2010). Dark-eyed Juncos breeding at 2,000 m also had 18% higher survival compared to those at low elevation on the same mountain (1,000 m; Bears et al. 2009). Pacific Wrens had the reverse pattern with low survival and breeding philopatry at high elevation. Wrens breeding at low elevation experienced an annual survival of 33%, similar to other wren populations (Peach et al. 1995, Hejl et al. 2002). However, none of the birds banded at high elevation returned the following year, suggesting either low survival or low site fidelity on high elevation territories.

It was not clear which key resources limit breeding for Pacific Wrens at high elevation. Nest sites may be limited at high elevation as they are predominantly associated with downed or dead wood (Waterhouse et al. 2002), which is limited at high elevation. Wrens are capable of nesting on cliff faces and other locations, and appear adaptable in their nest site selection. One male built five nests on his high elevation territory, and still failed to attract a mate suggesting that females may be reluctant to settle on high elevation territories. Food earlier in the breeding season may be limiting as insects and other invertebrates form the mainstay of their diet (Van Horne and Bader 1990, Hejl et al. 2002). Reduced time to breed within a season and greater stochasticity in environmental conditions at high elevations impose strong limits on annual fecundity, especially given the dual disadvantage of higher failure of first clutches and reduced opportunities for re-nesting and second broods compared to low-elevation populations.

We conclude Pacific Wrens lack adaptations to high elevation, and that upper montane and subalpine sites represent inferior breeding habitats. However, we observed hatch-year individuals and broods, indicating that a small proportion of Pacific Wrens bred successfully at our high elevations sites. Given that individuals and pairs also occur at high elevation elsewhere, it is reasonable to acknowledge that in some locations, years or habitat types, Pacific Wrens are able to reproduce successfully and survive at higher altitudes.

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