

Economy of mate attraction in the Cassin's finch

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Mate attraction can be costly. Thus, individuals should modulate it according to its probable benefits. Specifically, individuals should modulate mate-attraction efforts based on their need for, the probability of attracting, and the reproductive competence of prospective mates. We tested these predictions by monitoring song output in laboratory-housed male Cassin's finches (*Carpodacus cassinii*) before, during and after brief female exposure following variable periods of isolation from females. We inferred individual reproductive competence from the product of season and reproductive schedule, the latter estimated from moult progress. Males produced little song in the presence of a female but robustly elevated song output in response to female loss. However, mere absence of a female did not elevate song output in males unaccustomed to female proximity. Furthermore, song output in response to female loss increased with her reproductive competence. We suggest that individuals modulate mate-attraction effort based on the benefits such efforts are likely to yield.

Keywords: bird song; courtship; reproductive decisions; moult; reproductive schedule; seasonal breeding

1. INTRODUCTION

Male songbirds attract mates by singing (McGregor 1991). Because song production may incur costs (Gil & Gahr 2002), males should modulate it according to its probable benefits. For instance, song effort should decline once a mate has been attracted (Ball 1999) but increase if the male loses the mate (Krebs *et al.* 1980; Cuthill & Hindmarsh 1985). When a male is unlikely to attract a mate because candidates are scarce, song effort should be low. Finally, song effort should increase with female reproductive competence, which, at any one time, can vary widely among females owing to individual variation in reproductive schedule (Perrins 1970).

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Cassin's finches (*Carpodacus cassinii*) breed in mid- to high-elevation coniferous forests in the western USA (Samson 1976; Mewaldt & King 1985). Most songs are relatively stereotyped across males of a population (Samson 1978) and consist of a rapid series of short, 2–6 kHz syllables (Hahn 1996; see Electronic Appendix for details on song and other aspects of their natural history). Using wild-caught laboratory-housed Cassin's finches, we manipulated the duration of isolation from females, which varied in reproductive competence, to test the prediction that males adjust song effort in response to female availability and reproductive competence. Reproductive competence is a function of the interaction between season and reproductive schedule, the latter inferred non-invasively by the progress of post-breeding feather moult. In photoperiodic species, onset of moult presages the termination of reproductive competence (Dawson *et al.* 2001). By comparing moult-stages between females, we inferred whether a female's reproductive schedule was advanced or delayed relative to that of the other females. We predicted, for example, greater late-season song output in males courting delayed females than in those courting advanced females, because delayed females are more likely to still be reproductively competent.

2. MATERIAL AND METHODS

(a) Pre-experiment

On 31 October 2002, we captured 20 Cassin's finches in the Sierra Nevada, CA, USA (2300 m elevation; 37°50' N, 119°10' W). We held them at the University of California Davis on naturally changing photoperiods with *ad libitum* food and water and sexed them by laparotomy. On 14 January 2003, we transferred 10 males, determined by plumage to have hatched that spring or summer (Electronic Appendix), and 10 females of unknown age to single-sex sound-attenuation chambers, with three males and five females per chamber (except 1 male inadvertently housed with females; see §3a). We held them on an 8 h light:16 h dark photoperiod (8L:16D).

(b) Experiment procedure

On 23 August 2003, we changed the photoperiod to 15L:9D to stimulate reproductive physiology and behaviour, and initiated the experiment. We recorded each male's song during two trials. Each trial consisted of two consecutive days, one during which he was with the female randomly and uniquely assigned to him and the other during which he was alone. After three weeks, we completed trial 1 and began trial 2, recording males' song in the same order and each with the same female but with the female-presentation sequence reversed. Therefore, for half of the males, female-presentation sequence was present-absent-absent-present; and, for the other half, it was absent-present-present-absent (hereafter P₁A₁-A₂P₂ and A₁P₁-P₂A₂, respectively; subscripts indicate trial and letters indicate female presence or absence for each of the two days of a trial).

Birds were always transferred to the recording chamber 2.0–3.5 h after lights-on and remained there until 2.0–3.5 h after lights-on the following day (females), or two days later (males). We placed the female in a separate cage immediately beside the male so that he could see and hear but not have physical contact with her.

(c) Quantification and analyses

Using a Radioshack Pro-Unidirectional Dynamic microphone (catalogue number 33-3001) suspended 5 cm above the centre of the male's cage and a Sony TCM-5000EV analogue tape recorder (recording frequency, 90–12 000 Hz), we recorded song during the first hour following the addition or removal of a female for both days of both trials, yielding four 1 h recordings for each male. Using AVISOFT software (v. 4.1a), we digitized recordings at 8 bits and 22 050 kHz (time resolution, 5.8 ms; frequency resolution, 56 Hz).

On 17 November, three weeks after completion of trial 2, and again on 10 December 2003, we assessed moult progress of primary feathers as described previously (Hahn 1995), and separately ranked males and females from 1 to 10 (delayed-advanced schedule). None had begun moult during the experimental period but all were moulting on both assessment dates. The two dates' ranks were positively but not perfectly correlated (females: $F_{1,8}=16.75$, $p=0.003$, $r^2=0.677$; males: $F_{1,8}=13.40$, $p=0.006$, $r^2=0.626$), reflecting small changes in ranking during the three-week inter-assessment interval.

We analysed the number and total duration of songs (both log-transformed after adding 1 to homogenize variances; raw values graphically depicted) with respect to the presence or absence of a female, using repeated measures ANOVAs in which recording day was a within-subject factor and female-presentation sequence was a between-subjects factor. To investigate the effects of reproductive competence, we focused on the day immediately following female removal (A_1 for $P_1A_1-A_2P_2$ males and A_2 for $A_1P_1-P_2A_2$ males), when song output was generally high (see §3a). We used ANCOVAs in which the between-subjects variables trial and moult rank accounted for 'season' and reproductive schedule, respectively.

3. RESULTS

(a) Effects of female presence on male song

In the presence of a female, males sang very little (figure 1). Song output in their absence depended on recency of female exposure. In the 1 h immediately following removal of the female (A_1 of $P_1A_1-A_2P_2$ and A_2 of $A_1P_1-P_2A_2$), males sang prolifically. Males last exposed to females three weeks prior (A_2 of $P_1A_1-A_2P_2$) sang less; and males deprived of female exposure for seven months (A_1 of $A_1P_1-P_2A_2$) sang very little. The male inadvertently housed with females was tested in the $P_1A_1-A_2P_2$ sequence.

Statistically reflected in the day \times sequence interaction, this effect of recency of female presence was extremely reliable, regardless of whether our

dependent measure was seconds or number of songs (each measure: $F_{3,24}>31.47$, $p<0.000\ 01$).

(b) Effects of reproductive competence on male song

Reproductive competence is a function of the interaction between reproductive schedule and season. Therefore, we examined the effects of the moult rank \times trial interaction on song output in response to female loss (A_1 of $P_1A_1-A_2P_2$ and A_2 of $A_1P_1-P_2A_2$). The relationship between female moult rank and song output during trial 1 contrasted markedly with that three weeks later during trial 2, regardless of moult assessment date or whether the measure was seconds (17 November moult \times trial: $F_{1,6}=13.81$, $p=0.010$; 10 December: $F_{1,6}=14.79$, $p=0.008$) or number of songs (17 November: $F_{1,6}=7.43$, $p=0.034$; 10 December: $F_{1,6}=6.70$, $p=0.041$). Whereas the relationship between female moult and these measures of song output in trial 1 was positive, albeit unreliable (see *post hoc* linear regression results in figure 2), it was reliably negative three weeks later in trial 2. The effect of male reproductive competence on song output was unreliable (moult \times trial effect for each model: $F_{1,6}<1.01$, $p>0.2$).

4. DISCUSSION

The song behaviour of the male Cassin's finches in this laboratory study apparently functions primarily to attract females that are probably in the vicinity, as suggested by the strong propensity for males to sing in direct response to female loss, but not the mere absence or the presence of a female. Previous studies

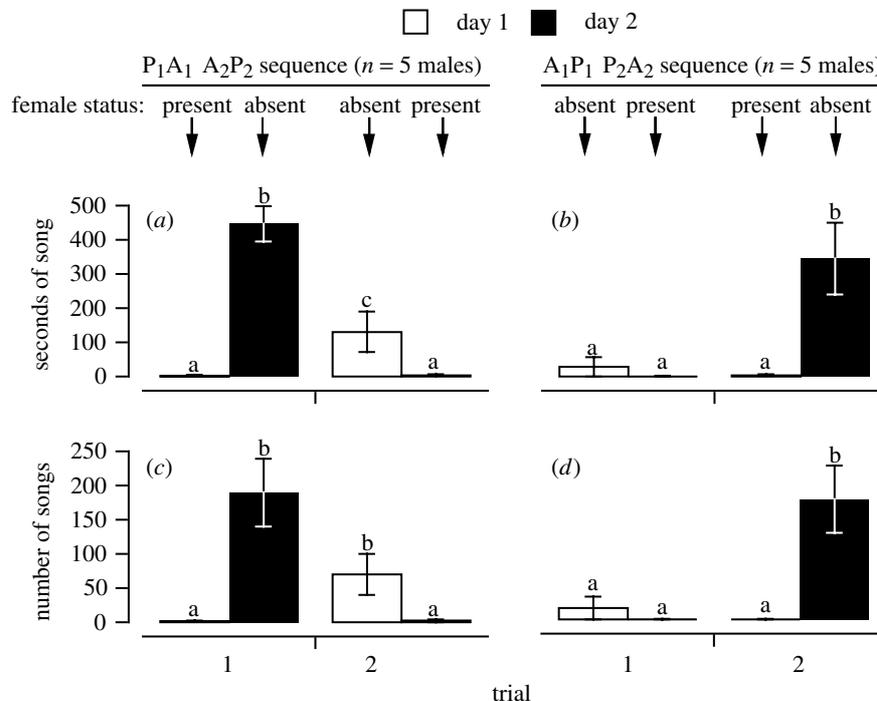


Figure 1. Song output, measured as seconds of song (a, b) and number of songs (c, d) in male Cassin's finches in response to female presence or absence (mean \pm s.e.m.). Song was recorded for 1 h on each of two consecutive days over two trials separated by three weeks. Males were exposed to females in the order present-absent (trial 1) absent-present (trial 2; a, c) or absent-present (trial 1) present-absent (trial 2; b, d). Within a panel, bars without a letter in common were reliably different ($p<0.05$) based on Fisher's least-significant-difference *post hoc* comparisons.

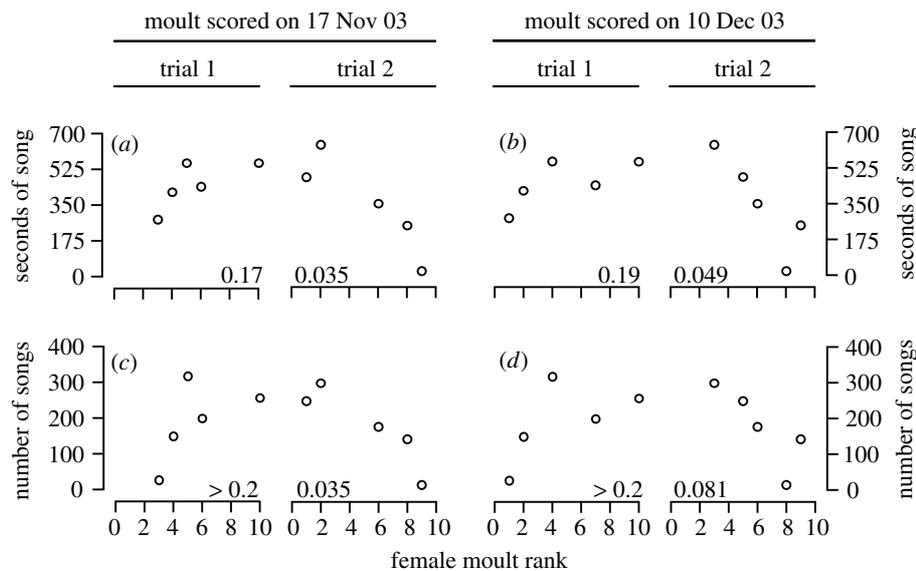


Figure 2. Song output, measured as seconds of song (*a, b*) and number of songs (*c, d*), in male Cassin's finches in response to the moult rank of the female just lost. Moult was scored on 17 November (*a, c*) and 10 December 2003 (*b, d*), several weeks after song was recorded, and females were ranked according to their moult progress on each date (1–10, delayed–advanced). Numbers at the bottom of each panel are *p*-values from *post hoc* linear regressions.

documenting a rise in male song output in response to mate loss (see §1) did not distinguish between loss of a mate and absence of a mate, or between the mate specifically and a nearby female. Here, we show that the longer males had been deprived of female exposure, the less they sang in their absence. Moreover, only one day of female visual and acoustic proximity was necessary to elicit a robust increase in song output in response to her loss.

Song output may depend on the reproductive competence of the female just lost. Early in the season, during trial 1, song output increased as the moult rank of the female just lost increased, although the repeatability of this increase is far from reliable. Three weeks later, during trial 2, song output showed a reliable decrease as moult rank of the female increased. Moreover, the effects of the female moult \times trial interaction indicate that the slope of the song–moult relationship consistently differs between trials and, therefore, that the seasonal change in the relationship between song output and the reproductive schedule of the female just lost is itself reliable, regardless of moult-assessment date.

Our inference that moult rank late in the season reflects the reproductive schedule hinges on the validity of three assumptions. First, moult onset must be associated with the termination of reproductive competence, which is marked by the onset of photorefractoriness in photoperiodic species (Dawson *et al.* 2001). Numerous studies have shown that onset of moult and photorefractoriness are tightly coupled and may be under the same physiological regulation (Dawson & Sharp 1998), confirming the validity of this assumption.

Second, inter-individual variation in rate of moult progress must be small, such that moult rankings reflect the order in which individuals lose reproductive competence. We did observe variation in moult rate, but the fact that moult scores on the first

assessment date yielded the same relationship with song output as those three weeks later suggests that, despite modest variation, rankings largely reflect the order in which individuals lose reproductive competence.

Third, the duration of reproductive competence must be similar among individuals, such that the order in which individuals lose reproductive competence reflects the order in which they gain it. It is indeed possible that the window of reproductive competence varies among individuals, particularly if they differ in age (Sockman *et al.* 2004). Variation in duration of reproductive competence may explain the reduced ability of moult rank to predict song output early in the season. Alternatively, males may not rely on female reproductive competence to gauge song output early in the season.

We found that male Cassin's finches produce song in proportion to the reproductive competence of the female they are attempting to attract. This dynamic modulation of mate-attraction effort, whereby males adjust behavioural output according to its probable dividends, would seem beneficial in situations where attracting a mate is costly.

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- Ball, G. F. 1999 The neuroendocrine basis of seasonal changes in vocal behavior among songbirds. In *The design of animal communication* (ed. M. D. Hauser & M. Konishi), pp. 213–253. Cambridge, MA: Bradford/MIT Press.
- Cuthill, I. & Hindmarsh, A. 1985 Increase in starling song activity with removal of mate. *Anim. Behav.* **33**, 326–335.
- Dawson, A. & Sharp, P. J. 1998 The role of prolactin in the development of reproductive photorefractoriness and postnuptial moult in the European starling (*Sturnus vulgaris*). *Endocrinology* **139**, 485–490.

- Dawson, A., King, V. M., Bentley, G. E. & Ball, G. F. 2001 Photoperiodic control of seasonality in birds. *J. Biol. Rhythm.* **16**, 365–380.
- Gil, D. & Gahr, M. 2002 The honesty of bird song: multiple constraints for multiple traits. *Trends Ecol. Evol.* **17**, 133–141.
- Hahn, T. P. 1995 Integration of photoperiodic and food cues to time changes in reproductive physiology by an opportunistic breeder, the red crossbill, *Loxia curvirostra* (Aves: Carduelinae). *J. Exp. Zool.* **272**, 213–226.
- Hahn, T. P. 1996 Cassin's finch (*Carpodacus cassinii*). In *The birds of North America*, No. 240 (ed. A. Poole & F. Gill). Philadelphia, PA: The Academy of Natural Sciences.
- Krebs, J. R., Avery, M. & Cowie, R. J. 1980 Effect of removal of mate on the singing behaviour of great tits. *Anim. Behav.* **29**, 635–637.
- McGregor, P. K. 1991 The singer and the song: on the receiving end of bird song. *Biol. Rev.* **66**, 57–81.
- Mewaldt, L. R. & King, J. R. 1985 Breeding site faithfulness, reproductive biology, and adult survivorship in an isolated population of Cassin's finches. *Condor* **87**, 494–510.
- Perrins, C. M. 1970 The timing of birds' breeding seasons. *Ibis* **112**, 242–255.
- Samson, F. B. 1976 Territory, breeding density, and fall departure in Cassin's finch. *Auk* **93**, 477–497.
- Samson, F. B. 1978 Vocalizations of Cassin's finch in northern Utah. *Condor* **80**, 203–210.
- Sockman, K. W., Williams, T. D., Dawson, A. & Ball, G. F. 2004 Prior experience with photostimulation enhances photo-induced reproductive development in female European starlings: a possible basis for the age-related increase in avian reproductive performance. *Biol. Reprod.* **71**, 979–986.

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ELECTRONIC APPENDIX

This is the Electronic Appendix to the article
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Appendix

In Cassin's finches (*Carpodacus cassinii*) (figure 1), male song can occur year-round, although it is concentrated during the breeding season. Cassin's finches produce two general types of songs. The vast majority of songs are of a type that is loud, stereotyped, rapid-cadence,



Figure 1. Male Cassin's finch (*Carpodacus cassinii*). Photograph by Monte M. Taylor.

and given while perched or, in the early breeding season, during gliding flight (figure 2). The syntax of these songs appears to be the same whether the birds are perched or flying (Samson 1976).

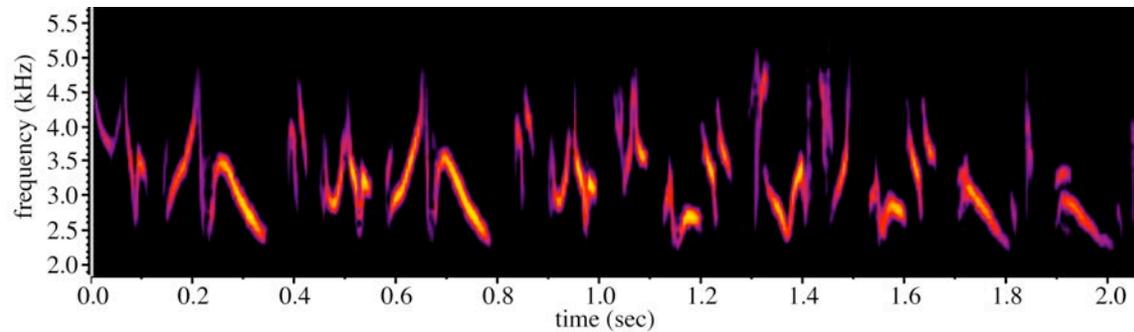


Figure 2. Spectrogram of stereotyped, rapid-cadence Cassin's finch (*Carpodacus cassinii*) song composed primarily of species-specific syllables. Color warmth reflects amplitude. In Adobe Acrobat, **click on the spectrogram to hear the song.**

The second general type of song is given only when perched (Hahn 1996). It differs syntactically from the stereotyped, rapid-cadence songs in being relatively slow cadence (i.e., longer pauses between song elements), very long (over 1 min in duration is not unusual), and in consisting almost entirely of heterospecific imitations occasionally interspersed with very high frequency (about 10 kHz) pure tones (figure 3). Whereas the stereotyped, rapid-cadence songs are loud and appear to occur during a variety of social contexts, including times when there are no other Cassin's finches in immediate proximity to the singer, the slow-cadence songs are often produced at very low amplitude and apparently only when another bird is very near. Slow-cadence songs may be particularly frequent immediately prior to copulations, but males have been observed seemingly directing them at other males. The vast majority (over 95%) of songs recorded in this study were of the stereotyped, rapid-cadence type (figure 2).

Mated males tend to cease singing entirely around the time their mates begin nest building, whereas unmated males continue singing for several weeks past the time most females begin nest building (Samson 1976). This, combined with the fact that males do not sing when aggressively defending their mates from other males (Samson 1976), suggests that song serves primarily a mate attraction function (Hahn 1996). However, it is possible that the two different song types, rapid- and slow-cadence, play different roles; the loud, rapid-cadence songs likely

function primarily in longer-distance, general advertisement for a mate, whereas the soft slow-cadence songs may function primarily in highly specific inter-individual interactions when a

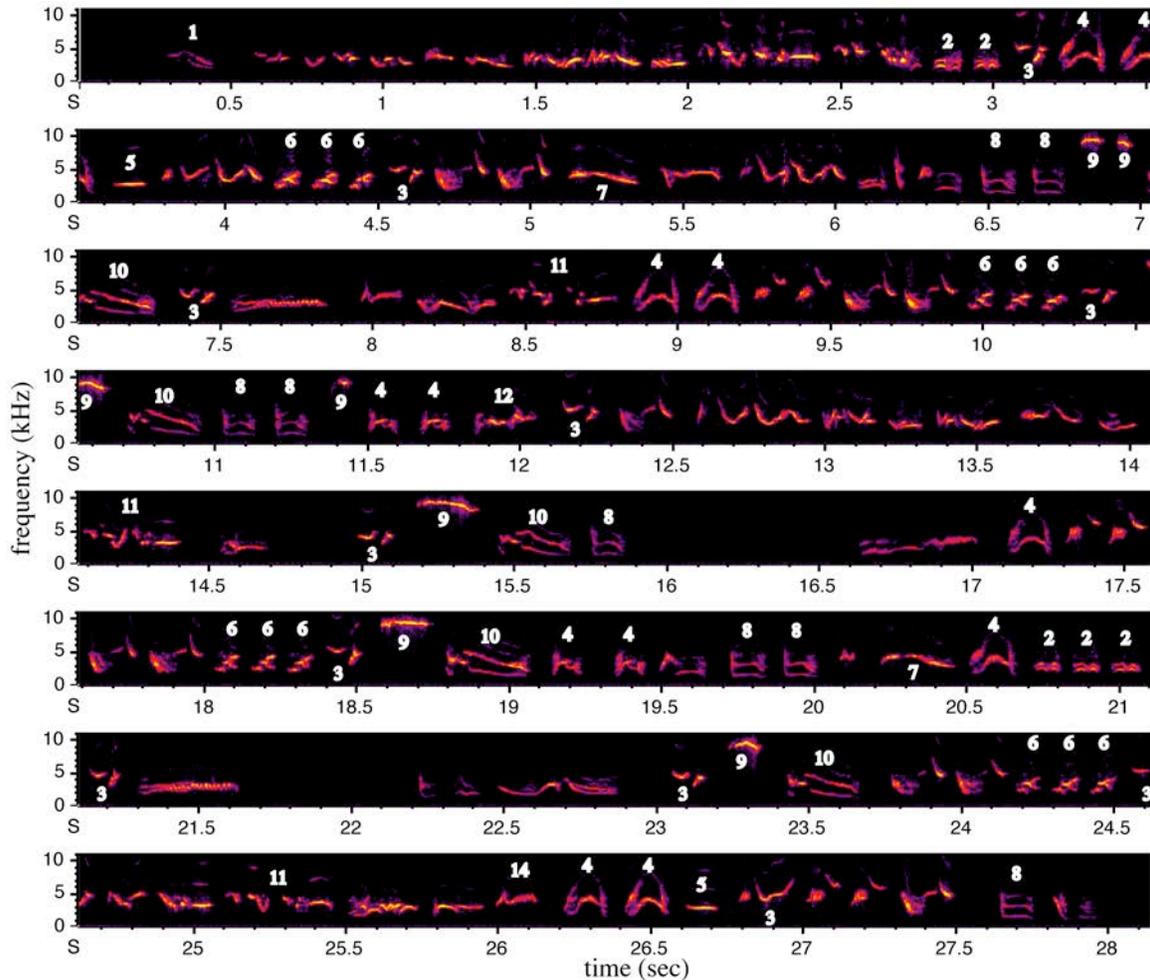


Figure 3. Spectrogram of slow-cadence Cassin's finch (*Carpodacus cassinii*) song composed of mostly heterospecific syllables. Color warmth reflects amplitude. In Adobe Acrobat, **click on the spectrogram to hear the song**. Numbered notes and note complexes were identified by ear as: 1, Cassin's finch "teew" call; 2, white-breasted nuthatch (*Sitta carolinensis*); 3, dusky flycatcher (*Empidonax oberholseri*); 4, American robin (*Turdus migratorius*); 5, Townsend's solitaire (*Myadestes townsendi*); 6, Steller's jay (*Cyanocitta stelleri*); 7, type II evening grosbeak (*Coccothraustes vespertinus*); 8, dark-eyed junco (*Junco hyemalis*); 9, Cassin's finch high "whistle"; 10, northern flicker (*Colaptes auratus*); 11, mountain chickadee (*Poecile gambeli*) "gargle"; 12, western tanager (*Piranga ludoviciana*); 13, pine grosbeak (*Pinicola enucleator*); 14 western wood-pewee (*Contopus sordidulus*).

mate or potential mate is in close proximity. An intriguing possibility is that rapid- and slow-cadence Cassin's finch songs are analogous to the "undirected" and "directed" songs, respectively, described for zebra finches (*Taeniopygia guttata*) (Zann 1996).

Cassin's finch breeding occurs in loose colonies in coniferous forests of the western United States. Dense breeding populations occur as low as about 1000 m in dry ponderosa pine (*Pinus ponderosa*) forests in the eastern Cascades of Washington State, up to around 3000 m elevation in lodgepole pine (*Pinus contorta*) forests of the Sierra Nevada in California (figure 4).



Figure 4. Representative Cassin's finch (*Carpodacus cassinii*) habitat in late spring at approximately 3000 m elevation in the Sierra Nevada, California, USA. Habitat is composed primarily of lodgepole pine (*Pinus contorta*) stands interspersed with wet clearings. Photograph by Keith W. Sockman.

Individuals appear to be socially monogamous (Samson 1976); there is no information regarding rate of extra-pair fertilizations. Males feed their mates during incubation, and females recognize individual-specific "feeding calls" produced by their mates. When incubating females hear their mate's feeding call, they fly to a perch near the nest to be fed, but they do not respond in this way to the feeding calls of other males (Samson 1978). Rather than defending fixed, all-purpose territories, males exclude other males from the area immediately surrounding their mate,

wherever she may be. The size of the defended area peaks at the time of clutch initiation. As noted above, song is not used as part of mate defence at this time.

Male Cassin's finches display delayed plumage maturation; yearling males achieve breeding condition while still in a drab, brown female-like plumage (Samson 1974). Their testes are fully competent, though averaging slightly smaller than those of older males. The sex ratio can be substantially male biased, and in some studies the brown, yearling males are less likely than the red, older males to acquire mates (Mewaldt & King 1985). It is unknown whether this mating bias is related to the immature plumage or to the somewhat less complex songs sung by yearling males (cf. Samson 1978).

Cassin's finch breeding schedules are highly seasonal and likely controlled strongly by photoperiod, although detailed studies remain to be performed. Breeding occurs only during the long days of late spring and early summer (Hahn 1996), and individuals become absolutely refractory to the stimulatory effects of long days (Hahn and MacDougall-Shackleton, unpublished data), like their close relative, the house finch (*Carpodacus mexicanus*) (Hamner 1968). Inter-annual variation in environmental conditions can lead to variation in timing of onset and termination of reproductive activity, on the order of a few weeks (Hahn 1996), and, for this reason, seasonal timing of singing activity varies somewhat among years (Samson 1976, 1978; Mewaldt & King 1985). Like most photoperiodic bird species, variation in timing of reproductive activity can also be attributed to inter-individual differences in reproductive schedule, as described in the present study.

REFERENCES

- Hahn, T. P. 1996 Cassin's finch (*Carpodacus cassinii*). In *The Birds of North America, No. 240* (ed. A. Poole & F. Gill). Philadelphia, PA: The Academy of Natural Sciences.
- Hamner, W. M. 1968 The photorefractory period of the house finch. *Ecology* **49**, 211-227.
- Mewaldt, L. R. & King, J. R. 1985 Breeding site faithfulness, reproductive biology, and adult survivorship in an isolated population of Cassin's finches. *Condor* **87**, 494-510.
- Samson, F. B. 1974 On determining sex and age in the Cassin's finch. *West. Bird Band.* **49**, 4-7.
- Samson, F. B. 1976 Pterylosis and molt in Cassin's finch. *Condor* **78**, 505-511.
- Samson, F. B. 1978 Vocalizations of Cassin's finch in northern Utah. *Condor* **80**, 203-210.
- Zann, R. A. 1996 *The Zebra Finch: A Synthesis of Field and Laboratory Studies*. Oxford: Oxford University Press.