

References

- Arnold, A. P. 1975. The effects of castration on song development in zebra finches (*Poephila guttata*). *J. Exp. Zool.*, **191**, 261–278.
- Bottjer, S. W., Miesner, E. A. & Arnold, A. P. 1984. Forebrain lesions disrupt development but not maintenance of song in passerine birds. *Science, N.Y.*, **224**, 901–903.
- Immelmann, K. 1969. Song development in the zebra finch and other estrildid finches. In: *Bird Vocalizations* (Ed. by R. A. Hinde), pp. 61–74. London: Cambridge University Press.
- Kroodtsma, D. E. & Canady, R. 1985. Differences in repertoire size, singing behavior, and associated neuroanatomy among marsh wren populations have a genetic basis. *Auk*, **102**, 439–446.
- Kroodtsma, D. E. & Pickert, R. 1980. Environmentally dependent sensitive periods for avian vocal learning. *Nature, Lond.*, **288**, 447–479.
- Nottebohm, F. 1969. The critical period for song learning. *Ibis*, **111**, 386–387.
- Pröve, E. 1983. Hormonal correlates of behavioral development in male zebra finches. In: *Hormones and Behavior in Higher Vertebrates* (Ed. by J. Balthazart, E. Pröve & R. Gilles), pp. 368–374. Berlin: Springer-Verlag.
- Thorpe, W. H. 1958. The learning of song patterns by birds, with especial reference to the song of the chaffinch *Fringilla coelebs*. *Ibis*, **100**, 535–570.

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Timber Wolf Howling Playback Studies: Discrimination of Pup from Adult Howls

Wolves (*Canis lupus*) produce a variety of structurally-variable howls to communicate with separated packmates and wolves of neighbouring, potentially hostile packs (Theberge & Falls 1967; Harrington & Mech 1978, 1979). To communicate effectively by howling, wolves must be able to distinguish between the howls of various classes (i.e. friend-foe, adult-pup, male-female, etc.). The purpose of the present study was to determine whether adults and pups distinguish between recorded adult and pup howls and if so, what kind of response is given to each class of stimulus. Data were collected from wolves of three free-ranging wolf packs in the Superior National Forest, Minnesota, at rendezvous sites between late July and mid-September.

Each playback session was a continuous period of 30 min to 2 hours spent near a rendezvous site. During each session, we monitored the radio-signals of any radio-collared animals present to determine their location and activity. An initial 15–30 min set-up period, while we set up the equipment and monitored signals, served as a control. The wolves never howled during this period. Playback

stimuli were then broadcast. Each stimulus was followed by a 10–20 min silent period, during which we recorded any howling that occurred (Sony TC-800B tape recorder, AKG D900E or Sennheiser MKH 816T microphone, at 19 cm/s). During most sessions, six playback stimuli were attempted at 10–20 min intervals, but weather, equipment problems, disturbance by humans, or approaches and retreats by the wolves introduced uncontrollable variation. All sessions were conducted between dusk and dawn, and most (65%) occurred between 1930 and 2400 hours. No more than one session was conducted per night per pack, with a median of 2 days (range 1–6) between sessions with any given pack.

Playback stimuli were 30–40-s-long series of pup or adult howls recorded during an earlier study (Harrington & Mech 1979). Each stimulus, composed of four to seven individual howls, was recorded from a different individual which was probably unfamiliar to all the animals tested in the present study. Adult howls were recorded from four males and one individual whose sex was unknown. Two stimuli were of excellent quality, one of intermediate quality, and two were of poor quality, characterized by noise and hiss. All but one pup stimulus were of excellent audio quality. Although all stimuli were used at least once, we decided to limit further playbacks to those of better quality.

Stimuli were broadcast using a Uher 4400 tape recorder, Realistic MPA-20 amplifier and a University Sound MLC or Atlas AP-30 loud-speaker. The initial stimulus class (pup or adult) for a session was determined randomly while equipment was being set up, and subsequent stimuli occurred in ABABAB or ABBAAB order. Each stimulus was broadcast in its entirety unless the wolves had begun howling, in which case the stimulus was terminated between individual howls.

Playbacks were conducted on 35 nights (1–15 sessions per pack-year) during which 241 playback stimuli were broadcast (2–17 per session; 28 sessions had between four and eight stimuli). Pup playbacks initiated 20 (57%) of the sessions. Stimulus position within a session had no effect on reply rate ($G = 6.66$, $df = 7$, $P > 0.60$; reply rate range was 50–74%), type of reply (percentage of group versus solo replies elicited: $G = 8.8$, $df = 7$, $P > 0.6$), number of solo howls elicited per stimulus, duration of group replies, or latency to reply for either group or solo replies (Kruskal-Wallis test: $P > 0.20$ for each pack for these temporal measures).

There were no significant differences in reply rate within or among packs for individual stimuli (Table I). However, the Perch Lake pack did reply

Table I. Frequencies of replies by wolves of three packs to playback stimuli

Stimulus	Pack			Stimulus	Pack		
	Adult howls	Gabbro Lake	Perch Lake		Wood Lake	Pup howls	Gabbro Lake
A	1/1*	—	—	F	1/4	—	1/3
B	9/13	3/5	3/3	G	7/21	6/8	2/11
C	8/14	5/6	4/7	H	4/12	5/10	3/9
D	28/33	8/9	11/17	I	2/6	3/5	0/4
E	3/3	7/7	—	J	5/14	5/6	1/5
				K/L	2/5	—	—
Totals	49/64	23/27	18/27		21/62	19/29	7/32
(%)	77%	85%	67%		34%	66%	22%

* Number of replies/total number of stimulus playbacks.

more often to each of the four pup stimuli that were presented to all three packs, and this trend was significant for the combined totals ($G=13.25$, $df=2$, $P<0.01$). The Perch Lake pack showed a non-significant tendency to be more responsive to individual adult stimuli.

The most consistent difference in reply rate occurred between adult and pup stimuli (Table I). For all three packs, the reply rate was greater for adult stimuli, and this difference was significant for both the Gabbro and Wood Lake packs ($G=24.04$ and 12.42 respectively, $df=1$, $P<0.001$). When sessions were analysed individually, the reply rate was greater for adult than pup stimuli on 27 occasions (77%), the same on seven (20%), and less than that for pup stimuli only once (3%).

Wolves approached us closely (within 5–15 m) during 11 sessions. Eighteen separate approaches were recorded; three sessions had two approaches and two sessions had three approaches. Between approaches on the latter five nights, the wolves returned to or near their original location, as deduced by radio-signals and/or replies to stimuli. Pup approaches followed adult stimuli nine times and pup stimuli only once. Pups only approached on nights when no adults or yearlings were present at the rendezvous site. Adult approaches followed adult stimuli six times and pup stimuli only twice. The one adult identified during an approach was an alpha male, while behaviours noted during the other approaches were those associated with alpha males during a previous study (Harrington & Mech 1979).

Both pup and adult wolves discriminate between pup and adult howls. The importance of adult howls to pups may be related to feeding; a pup slow to locate or be located by a returning adult may miss a meal. Pups were sometimes separated from

each other and were away from the usual centre of the rendezvous site when a session began (as indicated by their howling). In most cases, they returned to the centre prior to the next stimulus. Approaches to the playback site typically did not occur until several adult playbacks had been broadcast. Thus adult howls near a rendezvous site are not usually used to call the pups to the adult.

Adults were also very responsive to adult playback stimuli, both in terms of replying and approaching. Their replies may serve to protect the pups by warning strangers about the pack's location (Harrington & Mech 1979). Their approaches represent an escalated aggressive response to the close proximity and continued howling of the stranger (Harrington, in press). Overall, approaches by adults occurred more often during the present study (five of 17 sessions) than during a previous one (seven of 224 sessions; Harrington & Mech 1979), probably because we were closer to two of the rendezvous sites (100 m or less) during the present study than we usually were during the previous study (at least 100–200 m and usually 400–800 m away). Thus distance influences the type of response elicited by a stranger's howling (Voigt 1973; Harrington & Mech 1979), with approaches occurring most often when the threat posed by strangers is greatest.

The paucity of replies and approaches to pup playback stimuli suggests that neither adults nor pups recognized the pup playback howls as those of their own packmates, or that neither adults nor pups typically reply to the howling of packmate pups near the rendezvous sites. Data from the Perch Lake pack, which replied much more often to pup playbacks than did the other two packs, are relevant here. The Perch Lake playbacks were conducted far from the rendezvous site (greater

than 1 km), over a distance not normally traversed alone by pups of this age. The Wood Lake and Gabbro Lake pack playbacks, on the other hand, were conducted within 100 m of the rendezvous site, well within the usual range explored daily by pups of this age. As would be expected, only the former playbacks elicited relatively high reply rates.

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References

- Harrington, F. H. In press. Aggressive howling in wolves. *Anim. Behav.*
- Harrington, F. H. & Mech, L. D. 1978. Wolf vocalization. In: *Wolf and Man: Evolution in Parallel* (Ed. by R. L. Hall & H. S. Sharp), pp. 109–132. New York: Academic Press.
- Harrington, F. H. & Mech, L. D. 1979. Wolf howling and its role in territory maintenance. *Behaviour*, **68**, 207–249.
- Theberge, J. B. & Falls, J. B. 1967. Howling as a means of communication in timber wolves. *Am. Zool.*, **7**, 331–338.
- Voigt, D. R. 1973. Summer food habits and movements of wolves (*Canis lupus*) in central Ontario. M.S. thesis, University of Guelph, Ontario.

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Scanning for Predators in the Purple Sandpiper; a Time-dependent or Time-independent Process?

Several authors have argued that animals alternating between feeding and scanning for predators should scan randomly (Pulliam 1973; Bertram 1980; Elgar & Catterall 1981; Lendrem 1983a). The argument is that random scanning will prevent any attempt by the predator to predict the duration of inter-scan intervals during which it might make its final uncovered hunting approach. Recently, however, a number of authors (Lendrem 1983a, b; Hart & Lendrem 1984; Sullivan 1985) have observed

that birds do not scan randomly but instead avoid very short and very long inter-scan intervals. In this paper we show that these observations are consistent with a random, but time-dependent, model of scanning behaviour.

We start by treating scanning as a stochastic latency mechanism (see McGill 1967). The parameter of interest is the latency or delay between a bird putting its head down to feed and the first scan (the inter-scan interval). The stability of such a latency mechanism is reflected in its time constant λ . Traditionally it has been assumed that this remains fixed and that the random process determining latencies is time-independent. However, the observation that birds (such as ostriches) avoid very long inter-scan intervals (very long latencies) suggests that we are observing a time-dependent process. In other words we must replace the time constant λ with the time function $\lambda(t)$.

The kind of mechanism that we have in mind is one in which a bird puts its head down to feed and in which the probability of it looking up then increases with the time since it began to feed. Once it looks up the mechanism is reset ($\lambda(0)$). That is $\lambda(t)$ changes during an inter-scan interval but is not affected by the duration of earlier inter-scan intervals.

Perhaps the simplest case is that in which the probability of looking up increases as a linear function of time since the bird began to feed. That is

$$\lambda(t) = \lambda \cdot t \quad (1)$$

McGill (1967) has shown that the probability density of such a time function is given by

$$f(t) = \lambda t e^{-\lambda t^2/2} \quad (2)$$

This compares with

$$f(t) = \lambda t e^{-\lambda t} \quad (3)$$

for a random, but time-independent, stochastic process. The exponential distributions generated in tests of 'random' scanning (Bertram 1980; Elgar & Catterall 1981; Elcavage & Caraco 1983; Lendrem 1983b; Sullivan 1985) assume such a time-independent process.

In Fig. 1 we compare the cumulative frequency of inter-scan intervals for a solitary purple sandpiper (*Calidris maritima*) with the expected curves assuming (1) a time-dependent process and (2) a time-independent process.

The data were obtained by recording onto tape the moments when a purple sandpiper raised its head and scanned its surroundings and the moments when it lowered its head to feed (see Metcalfe 1984a). The inter-scan intervals presented here were obtained during a 20-min bout of undisturbed foraging on a musselbed. In this