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OFFSPRING DISCRIMINATION WITHOUT RECOGNITION: CALIFORNIA TOWHEE RESPONSES TO CHICK DISTRESS CALLS

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Abstract. Accurate offspring discrimination improves parental fitness by ensuring appropriate parental investment. In colonial avian species, offspring discrimination is often mediated by recognition of individual offspring vocalizations, but spatially segregated species do not necessarily need sophisticated recognition abilities if parents can use alternative information to distinguish offspring from nonoffspring. I experimentally tested the hypothesis that territorial California Towhee (*Pipilo crissalis*) parents use a location-based decision rule, instead of true vocal recognition of offspring, when deciding whether to respond to chick distress calls. Accurate responses to offspring distress calls should be favored by natural selection because they can have large fitness benefits if parents succeed in chasing away potential nest predators. Responses to nonoffspring, in contrast, may be costly and should not be favored by natural selection. Towhee parents were presented with a series of three playback experiments in which I manipulated the identity of the vocalizing chick, the age of resident chicks, and the location of the distress call broadcast. Parents showed no evidence of individual vocal recognition and no pattern of differential response to distress calls when offspring age differed from that of the calling chick. Parents did, however, exhibit a significant tendency to approach distress calls originating near their offspring more often than distress calls originating elsewhere on their territory. These results provide support for the evolution of an offspring discrimination strategy based on a simple location-based decision rule instead of true vocal recognition.

Key words: California Towhee, distress calls, offspring discrimination, offspring recognition, Pipilo crissalis.

Discriminación de la Progenie sin Reconocimiento: Respuestas de *Pipilo crissalis* a las Llamadas de Alerta de los Pichones

Resumen. La identificación precisa de la progenie por parte de los padres asegura una correcta inversión parental incrementando su adecuación biológica. En especies coloniales de aves, la identificación de la progenie se hace generalmente a través del reconocimiento de la vocalización. En especies con un patrón de segregación espacial, los mecanismos de reconocimiento no requieren ser muy sofisticados si los padres pueden usar otros mecanismos para reconocer a su progenie. De manera experimental, probé si los adultos territoriales de *Pipilo crissalis*, usan un mecanismo basado en la localización, en vez de un mecanismo auténtico de reconocimiento vocal, a la hora de responder a las llamadas de alerta de la progenie. La identificación precisa de las llamadas de alarma de la progenie debería ser favorecida por el proceso de selección natural, dado que al ahuyentar a los posibles predadores, los padres consiguen incrementar su adecuación biológica. La respuesta a llamadas de individuos no emparentados, sin embargo, puede ser costosa y no debería ser favorecida por el proceso de selección natural. Se expusieron a los padres a tres experimentos de playback en los que manipulé la identidad del pollo emisor, la edad de los pollos residentes y la localización de la llamada de alerta. Los padres no presentaron evidencias de reconocimiento de los individuos por su vocalización, así como ningún patrón de respuesta diferencial cuando los individuos diferían en edad. Sin embargo, los padres tendieron a aproximarse significativamente más a las llamadas de alerta emitidas cerca de su progenie que a las llamadas de alerta originadas en otros lugares de su territorio. Los resultados obtenidos apoyan la hipótesis de que el reconocimiento de la progenie se basa en un mecanismo simple de localización más que en un reconocimiento auténtico de vocalización.

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INTRODUCTION

Parents that can discriminate offspring from nonoffspring and accurately respond to offspring vocal signals may maximize individual fitness by ensuring that they provide valuable, potentially expensive parental care only to kin (Beecher 1981). Parental responses may be mediated by recognition of offspring vocal traits, but true recognition of individual calls may not be necessary to ensure appropriate response behavior. In particular, recognition capabilities may not have evolved in species where either the cost of recognition systems is high, or the benefit of recognition is low (Beecher 1991).

Comparative studies of species in which young from different families do and do not frequently mix provide a framework for theories of parent-offspring recognition. In her study of kittiwake nesting ecology, Cullen (1957) suggested that colonial species should have better developed parent-offspring recognition systems than solitary species. There is some evidence that colonial gulls such as Herring Gulls (*Larus argentatus*) show better parent-offspring recognition that noncolonial gulls such as kittiwakes (*Rissa* spp.), but results tend to vary across experiments (Cullen 1957, Storey et al. 1992). Other colonial seabirds also show strong parent-offspring recognition abilities, supporting the claim that recognition is important in such a setting (Tschanz and Hirsbrunner-Scharf 1975, Seddon and van Heezik 1993, Lefevre et al. 1998).

The best tests of parent-offspring recognition ability in relation to brood mixing come from several species of swallows. In colonial swallow species, where young birds mix regularly, parents recognize the calls of their own nestlings, but in solitary or territorial species such recognition systems have not evolved (Beecher et al. 1981a, 1981b, Stoddard and Beecher 1983, Medvin and Beecher 1986). Instead, because broods never mix, a simple, location-based decision rule for investing in young results in a sufficiently low error rate, both in terms of responding to unrelated offspring and failing to respond to their own young, and is apparently the superior fitness strategy (Beecher 1989, Sherman et al. 1997). Such a response rule would be costly in colonial settings if adults frequently wasted energy or put themselves in danger when responding to the distress calls of nonkin located near their own offspring. In contrast, a location-based response rule would be beneficial in spatially subdivided populations where broods are spaced far enough apart that nonoffspring would rarely, if ever, vocalize in the vicinity of offspring.

When captured or closely pursued by a predator, adults and chicks of some bird species emit loud calls that act as distress signals and may induce an approach response by conspecifics (Rohwer et al. 1976). Although several avian species can recognize offspring by vocal cues alone (Beecher et al. 1981a, McArthur 1982, Lefevre et al. 1998), such recognition has generally been related to begging behavior and has only once been shown to extend to distress call vocalizations (Chaiken 1992). In European Starlings (*Sturnus vulgaris*), chick distress calls are individually distinctive, and parents approach the distress calls of their own chicks more frequently than those of alien chicks (Chaiken 1992). Thus, distress calls may carry enough information to allow parents-offspring recognition.

Distress calls provide an excellent tool for examining parental vocal recognition abilities because distress call response behavior has clear fitness consequences for adults. Respondents may benefit by learning about a predator, helping to chase it away from themselves, or helping to chase it away from offspring (Hogstedt 1983). In contrast, failure to respond may result in the death of the signaling offspring and possibly its siblings. Although only European Starlings have been tested for true recognition of distress calls, theory predicts that, as with other vocalizations, solitary species may use simple decision rules instead of true vocal recognition systems to discriminate distress-calling young (Beecher 1989). I experimentally tested for the existence of parental discrimination of chick distress calls in California Towhees (*Pipilo crissalis*), a territorial avian species. A distress call signal could potentially carry a variety of cues that may be assessed when deciding whether to respond, including chick identity, chick age, and chick location. Because offspring do not naturally mix in this species, I predicted that natural selection would have favored simple decision rules over more complex recognition strategies.

METHODS

STUDY SYSTEM

All data reported in this paper are based on experiments and observations conducted between March 2003 and July 2005 at the Hastings Natural History Reservation in Monterey County, California, where I studied a population of over 200 color-banded California Towhees. The study site includes approximately 60 ha of oak woodland, including two creek drainages.

California Towhees are monogamous, territorial birds that raise up to five chicks at a time on nonoverlapping territories (Kunzmann et al. 2002). Neighboring pairs breed during a predictable spring season, but clutch initiation dates generally vary among neighbors. For example, in 2005, pairs in my study population initiated clutches as early as 13 April and as late as 8 June. Young birds stay on the parental territory for approximately a month after fledging, during which time they are fed and protected by their parents (Kunzmann et al. 2002). After this period, young birds disperse from their natal territories and parental care terminates. Because adults are territorial and aggressive toward conspecific intruders, nonoffspring fledglings are unlikely to be present on an adult's territory while it is caring for offspring. In 150 hr of observation time, I only twice observed fledglings on territories belonging to adults that were not their parents. In both instances the fledglings were at territory boundaries, accompanied by parents, and were chased away within 10 min (LB, unpubl. data).

California Towhees produce loud, piercing, scream-like calls that act as distress signals (Marshall 1964). Individuals produce discrete distress calls with fundamental frequencies around 5–6 kHz and durations of less than 1 sec. Birds in the hand that begin distress calling typically continue calling in long bouts. Distress calls are given most frequently by fledglings: 66% of fledglings in my study population ($n = 38$) gave distress calls on first capture, compared with only 18% of adults ($n = 118$). Fledgling distress calls are loud, reaching volumes up to 85 dB when measured using a sound level meter (Model #33-2055, Radio-Shack® Corporation, Fort Worth, Texas) positioned 0.3 m from the bird. Chicks in the nest under 10 days of age rarely produce distress calls (19%, $n = 63$), and when they do they give weak vocalizations that are audibly different from the loud calls of fledglings.

Field observations indicate that adult conspecifics rapidly approach fledgling distress calls and frequently vocalize nearby while chicks are calling (Quaintance 1941; LB, pers. obs.). During the breeding season, adult California Towhees will act aggressively toward a variety of potential predators, and they have been observed to successfully chase Western Scrub-Jays (*Aphelocoma californica*) away from nest sites (Childs 1948, Altmann 1956; LB, pers. obs.). Thus, timely response to chick distress calls may enable parents to effectively reduce threats to their offspring.

PLAYBACK EXPERIMENTS

When chicks produce distress calls, adults must make a rapid decision about whether or not to approach. To assess distress call recognition ability and differential response behavior in California Towhees, I conducted experiments based on manipulation of three variables: caller identity, chick age, and call location.

Playback experiments were conducted between June 2003 and July 2005. All manipulations employed playbacks of chick distress calls recorded in 2003 from six fledglings aged 29–39 days and resident on six different territories. Recordings were made with a Sennheiser shotgun microphone and a Sony TC-D5ProII cassette recorder. Recordings were captured at a sampling rate of 11 kHz and converted to digital files using program Syrinx (<http://syrinxpc.com>) and a Dell PC. Six separate playback tracks were used, each containing the vocalizations of a single fledgling. A playback track was constructed from one 30 sec long recording of a fledgling vocalizing repeatedly in a series of 21–27 distress calls. Playback tracks for the chick identity experiment contained three repeats of one 30 sec long recording, while playback tracks for the chick age and location experiments included four repeats of one 30 sec long recording. Calls were not spaced identically on all tracks, but were left untouched to reflect natural vocalization patterns. The time between calls ranged from a minimum of <1 sec to a maximum of almost 5 sec.

Playbacks were broadcast with a Radio-Shack® amplified speaker (#277-1008C) connected to a portable Panasonic compact disc

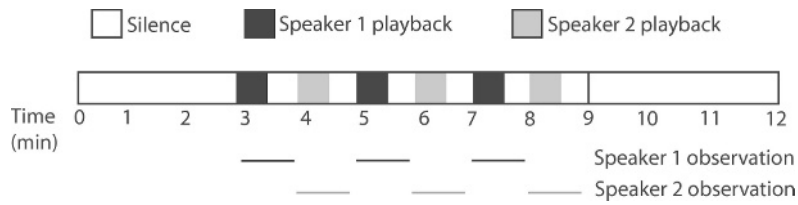

FIGURE 1. Timetable of distress call playbacks and data collection for each of 12 chick identity playback trials involving six pairs of California Towhees (*Pipilo crissalis*) at the Hastings Natural History Reservation, Monterey County, California. Adult California Towhee behavior toward both speakers was recorded during the 3 min of silence prior to and following playback. Behavioral data were recorded for each speaker during playback from that speaker and for 30 sec of silence immediately following playback from that speaker.

player. Playback distress calls were broadcast at a sound pressure level of 80 dB at 0.3 m. For each trial the speaker was placed at a height of approximately 1 m in vegetation bordering an open field or clearing. Two observers simultaneously monitored playback trials with a combination of video and audio dictation for later conversion into quantitative response measures including: responder identity, occurrence of an approach to within 10 m of the speaker, and time spent within 10 m of the speaker. Data were analyzed with nonparametric tests using JMP® version 5 (SAS Institute 2004). Unless otherwise indicated, values presented are means ± SD. Due to the complexity of the habitat, the location of focal territorial birds was not known when all trials began. Three experiments were performed to examine the roles of chick identity, chick age, and chick location in parental response to chick distress calls.

Chick identity. Chick identity experiments were conducted in June–July 2003 to test individual vocalization recognition abilities of parents. If California Towhees can recognize individual offspring vocalizations, they should approach the distress calls of their own offspring preferentially over the distress calls of foreign young.

Six sets of parents were given a preference test in which they were presented with one speaker playing distress calls recorded from their own fledged offspring and a second speaker playing distress calls recorded from unfamiliar nonoffspring of approximately the same age (within 10 days). Foreign chick distress calls were recorded on territories located at least 400 m and one intervening territory away from the focal territory. Each audio track was used once as an offspring stimulus on the focal territory and once as a nonoffspring stimulus on another territory.

For each trial, the two speakers were placed approximately 40 m apart and centered within the focal territory. Speakers and other observational equipment were put in place 2 hr prior to playback. During playback periods, the speakers would alternate broadcasting 30 sec of distress calls followed by 30 sec of silence (Fig. 1). Each speaker played three times. To ensure that responses were provoked by the broadcasting speaker, data were scored for each speaker only during playback and for the 30 sec immediately following. Thus, each trial lasted for 6 min, and data were scored for 3 min per speaker. Data were also scored for 3 min prior to and following playback to provide measures of baseline behavior.

Each territorial pair received playbacks at the same time on two successive days to control for location effects. On day one, the speaker location and order of presentation of local offspring vs. foreign nonoffspring distress calls was randomized. On day two, the playback audio tracks were switched between speakers and playbacks were repeated. Playbacks were conducted in the morning on three territories and in the late afternoon on the remaining three territories. Approach to within 10 m of the speaker by one or more California Towhees on the territory was scored as a positive response.

Chick age. Chick age experiments were conducted in May–July 2005. If California Towhees use age as a cue to offspring identity, they should not respond to distress calls when

there is a mismatch between caller age and offspring age. In the first of two trials, 12 pairs of California Towhees with chicks aged between two and five days of age were presented with playbacks of foreign distress calls recorded from chicks at least three weeks older than their offspring. Playbacks were repeated using the same audio tracks when focal chicks were between 23 and 27 days of age, and could produce distress calls similar to those used in playbacks. Due to brood loss, two pairs were not retested when they had older fledglings. Instead, to maintain sample sizes, two different pairs with older fledglings were tested with the relevant audio tracks.

For each playback trial, a speaker was positioned 5 m from the resident chicks. Trial periods consisted of 2 min of preplayback silence, 2 min of distress call playback, and 2 min of postplayback silence. Six audio tracks were used on two to three territories each over the course of the experiment. If a parent approached the speaker in either of the two trials it was scored as a responder. Fisher's exact test was used to test for a difference in response tendency by female and male parents. Fisher's exact tests were also used to compare rates of approach to within 10 m by at least one parent during the preplayback and playback periods, as well as across the two age groups. A Wilcoxon rank sum test was used to assess differences in the amount of time that at least one parent spent within 10 m of the speaker during playback.

Chick location. Chick location experiments were conducted on four territories in June 2004 and 12 additional territories in May–July 2005. These experiments tested the prediction that California Towhees use distress call location as a cue to the identity of the vocalizing chick, and should therefore respond only to distress calls that originate near their offspring. On two successive days, parents with chicks aged 23–27 days received playbacks of nonoffspring chick distress calls broadcast either 5 m from the focal chicks, or 5 m inside their territory boundary. Territory boundaries for all pairs were estimated based on trapping and resighting efforts during which birds were followed opportunistically to record movements around the area. The 16 experimental pairs were relocated 20.6 ± 8.8 times (range: 8–36) between 15 March and the initiation of playbacks each year. For the purposes of this experiment, territories were defined as areas of habitat that were used exclusively by a single pair. Playback locations at the center and edge of the territory were separated by an average of 44.0 ± 16.1 m (range: 16–69 m).

The same audio track was used for playbacks at the center and edge of each territory. Playback location order was randomized. Six audio tracks were used, each one on two to five different territories. Playback periods and data collection methods were the same as described above for the chick age experiments. Fisher's exact test was used to test for a difference in response tendency by female and male parents. Cochran-Mantel-Haenszel tests were used to compare rates of approach to within 10 m by at least one parent during the preplayback and playback periods, as well as across the two locations. A Wilcoxon signed rank test was used to assess differences in the amount of time that at least one parent spent near the speaker during playback.

Parents tested in both the chick age and chick location manipulations heard the same audio track in both experiments. Post-hoc statistical analysis of differential response by different pairs to the different audio tracks is not informative because of the small number of pairs exposed to each distress call sample, but all audio tracks were effective in provoking responses in at least one trial by 50%–100% of tested pairs.

CALL PROPAGATION TESTS

To assess whether adult California Towhees could hear distress calls played at the edges of their territories, I tested the sound propagation properties of two playback tracks recorded from two fledglings. These trials were performed 5 September 2006 in Tilden Park, Berkeley, California, in habitat similar to that found at the Hastings Reservation study site. Sound pressure levels of two recordings played at the experimental volume of 80 dB at 0.3 m were measured every 10 m to a distance of 120 m. A linear correlation between sound pressure levels of the two tracks at each distance was calculated to ensure that distress call playbacks propagated similarly. Additionally, a blindfolded human observer listened for playback at distances up to 120 m.

RESULTS

CHICK IDENTITY

At least one adult California Towhee on each territory ($n = 6$) responded to at least one playback trial. During the 12 preplayback control periods I twice observed birds within 10 m of the speaker, but neither bird showed any detectable interest in the speaker. During playback periods, 8 of 12 trials (66%) elicited approach responses from one or more birds. Respondents would typically approach soon after distress calls began to play and would hop around several meters from the speaker in an agitated manner.

California Towhees could show one of four general approach responses to each trial: they could approach the speaker playing local distress calls only, they could approach the speaker playing foreign distress calls only, they could move back and forth to approach both speakers, or they could approach neither speaker. The six pairs tested showed highly variable combinations of these potential responses (Table 1). There was no consistent pattern of approach in first trials, no consistent pattern of approach in second trials, and no consistent change in approach behavior between first and second trials. Three of six pairs responded during trial 1, and five of six pairs responded during trial 2. Two pairs approached speakers during both trials, but they showed different response patterns in their respective first trials: pair C approached the foreign, unfamiliar distress call in trial 1 and the local offspring distress call in trial 2, while pair D approached the local distress call in both trials. Pair D was the only pair to show a consistent response in both trials. Across both trials, two pairs approached only the speaker playing foreign calls, two pairs approached only the speaker playing local calls, and two pairs approached both speakers.

TABLE 1. Approach response patterns of adult California Towhees (*Pipilo crissalis*) during chick identity playback preference tests. Trials were conducted on six territories (A–F) at the Hastings Natural History Reservation, Monterey County, California. "Local" distress calls were recorded from a chick resident on the experimental territory and "foreign" distress calls were recorded from a chick resident on a territory located at least one intervening territory away from the experimental territory. During a trial, one speaker broadcast a local distress call and the other broadcast a foreign distress call in an alternating pattern. Local and foreign playback tracks were swapped between speakers between trials 1 and 2 for each pair. Adult California Towhees showed no tendency to approach local distress calls over foreign distress calls, as would be predicted if parents recognized offspring distress calls.

Pair	Trial	Speaker approached
A	1	Neither
	2	Both
B	1	Neither
	2	Local
C	1	Foreign
	2	Local
D	1	Local
	2	Local
E	1	Neither
	2	Foreign
F	1	Foreign
	2	Neither

CHICK AGE

11 of the 14 (79%) male parents and 9 of the 14 (64%) female parents approached to within 10 m of the speaker during at least one trial. There was no significant difference in tendency to approach between the sexes (Fisher's exact test, $n = 28$, $P = 1.0$). When chicks were 2–5 days old, parents approached to within 10 m of the speaker in 10 of 12 trials (83%) compared to 7 of 12 (58%) trials when chicks were 23–27 days old. Both approach rates were significantly higher than those observed during preplayback control periods (Fisher's exact tests, $n = 24$, $P < 0.05$), but did not differ significantly from each other (Fisher's exact test, $n = 24$, $P = 0.37$). During playback, adults spent similar amounts of time within 10 m of the speaker regardless of chick age (Fig. 2). When chicks were young, parents collectively spent a mean of 82 ± 45 sec near the speaker and when chicks had fledged, parents spent a mean of 55 ± 57 sec in the area. Differences were not significant (Wilcoxon $z = -0.9$, $P = 0.36$).

CHICK LOCATION

9 of the 16 (56%) male parents and 7 of the 16 (44%) female parents tested approached to within 10 m of the speaker during at least one trial; there was no significant difference between the sexes (Fisher's exact test, $n = 32$, $P = 0.48$). Parent California Towhees approached

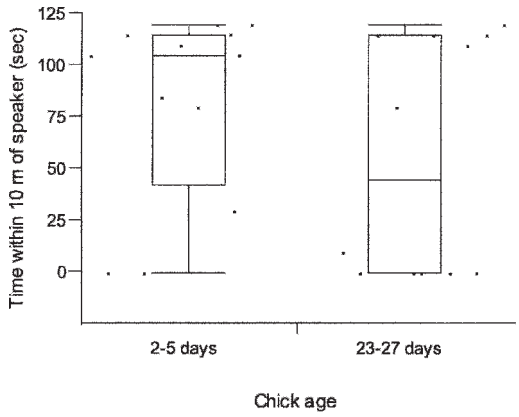

FIGURE 2. Time spent within 10 m of the speaker by at least one member of 14 California Towhee (*Pipilo crissalis*) pairs during playback of unfamiliar chick distress calls. Calls were played 5 m from young chicks aged 3–5 days (12 trials) and fledglings aged 23–27 days (12 trials) on 14 territories at the Hastings Natural History Reservation, Monterey County, California. Each black square represents a value for one pair, and squares are scattered horizontally within age classes only to improve figure readability. Box plots indicate median values and interquartile ranges. Differences between the two groups are not significant (Wilcoxon $z = -0.9$, $P = 0.36$).

to within 10 m of the speaker in 10 of 16 (63%) trials where distress calls were broadcast 5 m from their chicks. When distress calls were broadcast near the territory boundary, parents approached to within 10 m of the speaker in 2 of 16 (13%) trials. Distress call playbacks broadcast near the chicks elicited approach responses significantly more frequently than both the preplayback silence (Cochran-Mantel-Haenszel, $n = 32$, $P < 0.05$) and the playbacks near the territory edge (Cochran-Mantel-Haenszel, $n = 32$, $P < 0.05$). The time spent within 10 m of the speaker also differed between playback locations (Fig. 3). Collectively, parents spent a mean of 58 ± 54 sec near speakers at the center of the territory and 10 ± 28 sec near speakers at the edge of the territory. (Wilcoxon $t_{15} = 27.5$, $P < 0.05$).

CALL PROPOGATION TESTS

Sound propagation experiments revealed that the two playback track sound pressure levels declined nearly identically with distance ($r^2 = 0.97$, $P < 0.001$). Distress calls played at the experimental volume were audible to the human ear at 120 m, a distance far greater than the average of 44 m separating the two playback locations. At 120 m, playback sound pressure level was 25 dB. Passerines can detect sounds in the frequency range of chick distress calls (3–5 kHz) at volumes less than 20 dB (Dooling 1982), suggesting that playback was audible at distances greater than 120 m.

DISCUSSION

California Towhees showed no evidence of individual distress call recognition. Adults approached playback speakers indiscriminately, with an equal tendency to approach offspring and nonoffspring distress calls. Despite low sample sizes, approach behaviors were clear-cut and two-thirds of pairs approached foreign, nonoffspring distress calls in at least one trial. In chick age experiments, male and female parents approached foreign chick distress calls played near their own offspring regardless of offspring age. In chick location experiments, male and female parents approached distress calls originating close to their offspring and ignored distress calls originating elsewhere on their territories. This response bias was not due to inaudibility of playback, as sound propagation tests indicated that experimental pairs should have been able to hear distress calls played at territory boundaries from virtually anywhere on their territories. Additional experiments would be valuable, particularly recognition tests with increased sample sizes and age discrimination tests using playback of distress calls from differently aged chicks, but the data presented here provide several clear results regarding parental response to chick distress calls.

First, the results failed to support the recognition hypothesis prediction that parents will preferentially approach the distress calls of their own offspring. This suggests that adult California Towhees do not recognize individual distress call vocalizations or, if they do, they do not discriminate on this basis. Thus, the data suggest that California Towhee offspring recognition mechanisms differ from those of European Starlings, the only other species in which chick distress call recognition has been similarly tested. European Starlings do discriminate between the distress calls of offspring and unrelated chicks (Chaiken 1992). European Starlings are, however, semicolonial breeders,

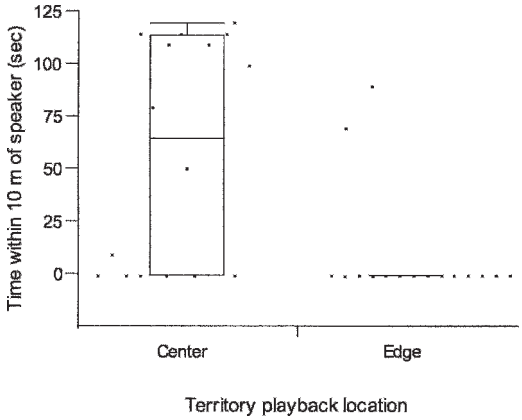

FIGURE 3. Time spent within 10 m of the speaker by at least one member of 16 California Towhee (*Pipilo crissalis*) pairs during playback of unfamiliar chick distress calls. Calls were played 5 m from fledglings and 5 m from the territory edge during 32 paired trials on 16 territories at the Hastings Natural History Reservation, Monterey County, California. Each black square represents a value for one pair, and squares are scattered horizontally within location classes only to improve figure readability. Box plots indicate median values and interquartile ranges. Adults spent significantly more time within 10 m of speakers playing distress calls near the center of their territories than they did within 10 m of speakers playing distress calls near territory boundaries (Wilcoxon $t_{15} = 27.5$, $P < 0.05$).

where similarly aged fledglings from multiple broods frequently mix, and parent-offspring recognition ability is well developed by the time young fledge at around 20 days of age (van Elsacker et al. 1988). Thus, individual chick distress call recognition patterns in these two species support the hypothesis that coloniality may drive parent-offspring recognition ability (Cullen 1957, Beecher 1989).

If noncolonial species fail to recognize offspring vocalizations, they may still discriminate offspring from nonoffspring using alternative cues. Two of the most obvious potential cues to offspring identity are age and location. In species such as the California Towhee, where neighboring pairs breed somewhat asynchronously, chick age may be a reasonable indicator of identity. This is particularly true when assessing vocalizations like distress calls, which change significantly throughout the nestling period and may provide a strong signal of age (LB, unpubl. data). Results of playback experiments, however, indicate that age is apparently not a cue used by adult California Towhees when deciding whether to approach chick distress calls. Parents did not respond to a mismatch in age between their own chicks and the vocalizing chick. It is possible that although age cues could be informative, they are more difficult to assess or less reliable than other cues, so the use of other cues has been promoted instead. Alternatively, age cues may not be informative. California Towhees are highly territorial birds that sometimes raise multiple broods in a season, so differently aged chicks on one territory would almost always be siblings from different nests (Kunzmann et al. 2002). In such a situation, parents would generally benefit from responding to distress calls of differently aged chicks.

Location was the one tested cue on which California Towhees appeared to base distress call responses. Parents were clearly able to assess both distress call location and offspring location. Approach responses occurred only when a distress call originated from a limited area around the chicks, suggesting that adult California Towhees use a highly refined, location-based decision rule in responding to distress calls. Chick location determined parental behavior, a result that is consistent with existing theory and empirical data from other territorial and solitary species. For example, noncolonial Barn Swallows (*Hirundo rustica*) and Northern Rough-winged Swallows (*Stelgidopteryx serripennis*) accept and feed any chick in their nests, apparently using location as a cue to chick identity (Beecher 1981, Medvin and Beecher 1986).

Why will California Towhee parents respond to any distress call played near their chicks? Adults that approach distress calls may benefit either by directly aiding their chicks, or by learning about a potential predator. A location-based decision rule might cause parents to sometimes respond to distress calls of nonoffspring, but such a situation is unlikely to arise because of the territorial nature of this species. If, however, parents did occasionally respond to an unrelated individual distress-calling on their territory, they might still benefit by learning about a real threat near their young, and they would only infrequently pay the cost of responding inappropriately. This pattern contrasts with the situation for a colonial species, where responding to every chick call near the

nest site would impose a frequent cost on adults.

Results of the experiments reported here suggest that distress call response strategies used by both male and female California Towhees are similar to offspring discrimination strategies used by other noncolonial species assessing different vocalizations (Medvin and Beecher 1986). When young from multiple broods rarely mix, parents can differentiate offspring from nonoffspring using a simple, but effective, location-based decision rule.

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