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

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A a . 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 (*a*) 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

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 (*a a a*) show better parent-offspring recognition that noncolonial gulls such as kittiwakes (*a* 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

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 (= 38) gave distress calls on first capture, compared with only 18% of adults (= 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%, = 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 (*A h. a a a*) 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 (5 http://syrinxpc.com 4) and a Dell PCt.64876I(six)93p6pdAdA,

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

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

RESULTS

CHICK IDENTITY

At least one adult California Towhee on each territory (= 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

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

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 (*H a*) and Northern Rough-winged Swallows (-) 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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