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Coyote Flight Movements Relative to Territory Boundaries: An Experiment in the Field

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ABSTRACT.—It is well-known that coyotes maintain exclusive territories in which they are least vulnerable to mortality from humans. Studies also indicate that resident (*i.e.*, non-dispersing) coyotes rarely leave these secure areas when unperturbed. Here, we investigated whether coyotes would maintain their fidelity to territories in the face of human pursuit. We used radiotelemetry to determine approximate territorial boundaries of six coyotes, and then attempted, via on-foot pursuit, to drive these individuals in a straight line, causing them to vacate their territories. Coyotes generally did not allow us to push them in a straight line beyond their territories, but instead doubled back as they approached territory boundaries. In contrast, a transient coyote fled from pursuit in a straight line for a distance equivalent to two or three territory diameters before we ceased pursuit. These findings suggest that coyotes perceive the security of their territories to be sufficiently great as to outweigh advantages of outdistancing their pursuer via straight-line flight.

INTRODUCTION

Coyotes (*Canis latrans*), like other canids, exhibit territorial space use (Camenzind, 1978; Kleiman and Brady, 1978; Bowen and Cowan, 1980; Wells and Bekoff, 1981). Territories are necessary for reproduction and likely confer a significant survival advantage to residents (Messier and Barrette, 1982; Sacks *et al.*, 1999b; Gese, 2001). Coyotes are rarely trapped (*i.e.*, by conventional trapping methods or infrared-triggered ''photo-capture'') in the interiors of their territories (Windberg and Knowlton, 1990; Sacks *et al.*, 1999a; Sequin *et al.*, 2003). Furthermore, territorial resident coyotes have higher survival rates than transients, which do not maintain territories (Windberg *et al.*, 1985; Gese, 2001). A likely explanation for the elevated vulnerability of coyotes outside their territory is a relative lack of familiarity and reduced ability to recognize hazards. The focus of this study was to develop a better understanding of the behavior of territorial coyotes relative to their territory space and boundaries.

At present, much of the coyote range occurs in human-dominated landscapes, where survival is most impacted by human activities associated with predator management or hunting (Windberg *et al.*, 1985; Knowlton *et al.*, 1999). We hypothesized that coyotes living in such a human-impacted landscape recognize the relative safety of their territories and, correspondingly, we predicted that resident coyotes fleeing human pursuit would remain in their territories rather than leave them to put more distance between themselves and a pursuer. Here, we experimentally tested this prediction via close-range, on-foot pursuit of radio-collared coyotes.

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STUDY AREA

We conducted the study May 1996–Oct. 1997 at the Hopland Research and Extension Center (HREC; 39°00′N, 123°05′W), a 21.7-km^2 research facility of the University of California, located in the North Coast Range of California. The HREC was characterized by a mosaic of annual grassland, chaparral, oak woodland, and mixed evergreen-deciduous forest covering a hilly to rugged topography of 150 m to 900 m in elevation (Murphy and Heady, 1983).

The HREC was the largest sheep operation in Mendocino County, and the coyote population experienced high human activity and human-caused mortality related to sheep ranching activities and depredation management. Consequently, coyotes on the study area were wary of humans. The study area was saturated with small, mutually-exclusive coyote territories; transient individuals were often located in the interstitial spaces between territories (Sacks *et al.*, 1999b; Blejwas *et al.*, 2002).

METHODS

As part of a broader study (1993–1998), the coyotes used in this experiment were captured, fitted with radio collars, and radio tracked beginning Nov. 1995 (Blejwas *et al.*, 2002). Capture and handling of coyotes followed Animal Care and Use protocols (University of California at Berkeley, R190-1496; USDA National Wildlife Research Center, QA-267). Methods for coyote capture and handling, radio telemetry methods and accuracy and home range calculation were detailed elsewhere (Neale *et al.*, 1998; Sacks *et al.*, 1999b).

Baseline (*i.e.*, pre-experiment) home ranges [90% adaptive kernel (AK) isopleth (Worton, 1989)] and core areas (65% AK isopleth) were estimated using program CALHOME (Kie *et al.*, 1996) for each of 6 radiocollared residents (3 adult males, 1 male pup, 2 adult females) based on radiolocations ($n > 100$) collected during the 2–6 mo prior to experimental pursuit. The 90% AK isopleth was used as an approximation of the territory border. Two adult male transients were also monitored during this period.

Experimental pursuit of each coyote was performed during daylight periods totaling 2–10 h over 1–2 d under cool and clear weather conditions. One person pursued the target individual on foot while 2–3 others located the animal from a distance using radio telemetry, taking simultaneous bearings (via radio communication) from known locations on roads. These trackers attempted to maintain locations at sufficient distance from the coyote (usually ~1 km) and, during pursuit of resident individuals, territory borders, so as not to bias coyote movements. The pursuer also used radio-tracking equipment to follow the target coyote. The radiocollars were equipped with activity sensors that enabled observers to distinguish three activity states: resting (slow, steady signal), running (fast, steady signal) and active (mixed signals). Locations were recorded when the coyote was moving as well as when it stopped to rest. When the pursuer spotted the coyote, these locations also were recorded by plotting on a topographical map carried in the field.

The initial flush involved approaching a resting animal until it became active. The pursuer then attempted to approach the subject along the same path it had taken, as though to push the coyote in a straight line. Pursuit resumed some time after the coyote settled into a resting location; the time required for the pursuer to reach the subject varied with distance and terrain (often >1 km in thick brush). Pursuit typically concluded at dusk or when an animal left the study area (which only occurred with transients).

RESULTS

During pursuit, most locations of resident coyotes were inside their core areas, and nearly all locations were contained within residents' territories (Fig. 1). Exceptions were locations

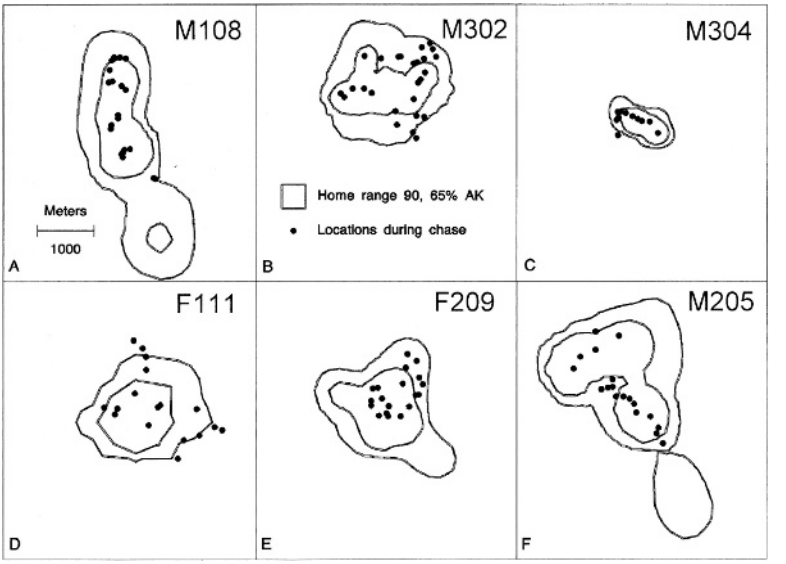

FIG. 1.—(A–F). Locations of six resident coyotes during on-foot pursuit, overlaid on home ranges and core areas, Hopland Research and Extension Center, Hopland, CA, Nov. 1995–Oct. 1997. A. Male (M) 108. B. M302. C. M304. D. Female (F)111. E. F209. F. M205

occurring just outside the 90% AK border (which did not necessarily reflect the precise location of the territory boundary). These represented turning-around points, after which the coyote moved back inside home range boundaries (Fig. 2). All residents displayed at least one instance of ''doubling-back'' from the boundary (or just outside it) towards territory interiors. In contrast, the two transient coyotes moved in a straight line away from the pursuer. In both cases, pursuit of transients ceased because they left the study area and moved onto private property where they could no longer be tracked.

DISCUSSION

Previous researchers have investigated coyotes' responses to human disturbances at greater temporal and spatial scales, *e.g.*, documenting contractions, expansions, and shifts in home ranges in response to disturbances such as military operations (Gese *et al.*, 1989). However, immediate responses of coyotes—in terms of movements relative to territory space—to acute human threat have not been investigated.

Here, the response of resident coyotes to an acute disturbance demonstrated the integrity of territory boundaries and supported our predictions. Resident coyotes, when pursued, moved away from the pursuer but doubled back when they reached the borders of their home ranges. This behavior by residents suggested that the perceived benefit of staying in familiar areas outweighed the perceived cost of proximity to threat (the pursuer in this case).

In contrast, transient coyotes moved in a straight line away from the pursuer, in one case covering a much greater linear distance than any of the residents. Although this example constitutes insufficient evidence to draw inferences about the behavior of transients in general, it does serve to validate our methodology with respect to the residents. That is, we

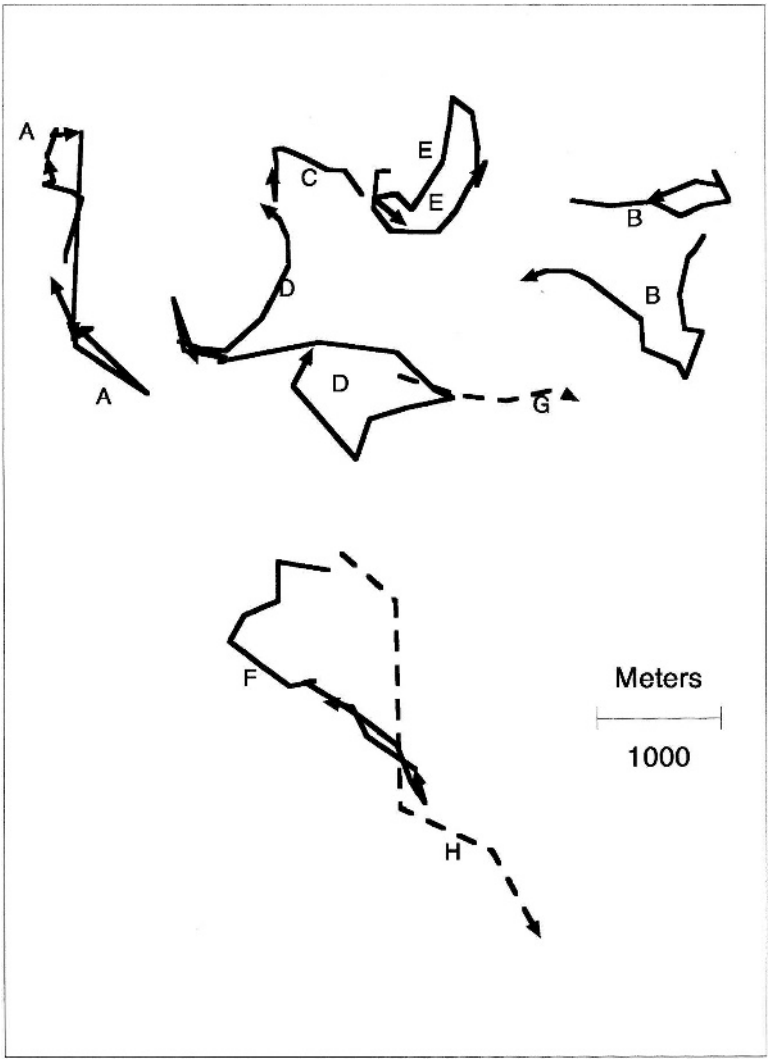

FIG. 2.—Movement of six resident (A–F, solid lines) and two transient (G,H, dashed lines) coyotes during on-foot pursuit, Hopland Research and Extension Center, Hopland, CA, May 1996–Oct. 1997. Locations connected by lines and direction of movement indicated by arrows. A. Male (M) 108. B. M302. C. M304. D. Female (F)111. E. F209. F. M205. G. M306. H. M112

were able to drive a coyote in a relatively constant direction in the absence of a reason for the individual to double back (*i.e.*, the territory boundary).

Lastly, we observed a tight correspondence between territory boundaries and limits to movements of resident coyotes. The discrete nature of these borders is in agreement with previous field observations of coyote territorial defense and scent-marking behavior indicating distinct territorial limits recognized by both territory holders and outside conspecifics using visual and especially olfactory cues (Camenzind, 1978; Bowen and Cowan,

1980; Wells and Bekoff, 1981; Harris, 1983). Alertness of coyotes appears to increase when coyotes approach the boundary of their territory (Camenzind, 1974). The territory border is where chases of intruders by resident pack members end and where a preponderance of scent-marking occurs (Allen *et al.*, 1999; Gese, 2001) and regular maintenance of territorial boundaries may be required in order to prevent take-over of territorial space by neighbors and transients (Gese, 1998).

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