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CRUISE FORAGING OF INVASIVE CHAMELEON (*CHAMAELEO JACKSONII XANTHOLOPHUS*) IN HAWAI'I

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ABSTRACT. We quantified the foraging behavior of the Jackson's chameleon (*Chamaeleo jacksonii xantholophus*), an invasive insectivorous lizard species in Hawai'i. Using video taken in the field, we focused on percent time moving, moves per minute, and movement speeds. Our results supported previous findings that chameleons are "cruise foragers" (*sensu* Butler, 2005), a foraging behavior unlike almost all other species of lizards.

KEY WORDS: foraging mode; behavior; chameleon; Hawai'i; invasive species

Classically, lizard feeding behavior has been described in terms of foraging mode, i.e., how an animal gathers food in a particular environment (e.g., Huey and Pianka, 1981; Schoener, 1971). Foraging mode is an important aspect of a species' predator–prey interactions and can affect prey behavior and community structure (Schmitz, 2008; Simmons *et al.*, 2005). Previous studies have identified two distinct foraging modes in lizards: active and ambush (sit-and-wait) foraging (Huey and Pianka, 1981; McLaughlin, 1989; Regal, 1983; Schoener, 1971). Other researchers have suggested a continuum with active and ambush foraging as opposite extremes (e.g., Anderson, 2007; Cooper, 2005, 2007; Cooper *et al.*, 2001; Perry, 1999; Perry and Pianka, 1997; Tollestrup, 1980). Evidence also suggests that foraging mode is retained in related species (Johnson *et al.*, 2008; Perry, 1999). Both active and ambush foraging behaviors can be associated with a suite of organismal traits, including morphology, behavior, habitat use, and prey type (Miles *et al.*, 2007; Perry *et al.*, 1990; Vitt and Congdon, 1978). For example, some active foragers have higher activity levels, caloric intake, and body temperatures compared with ambush foragers (Anderson and Karasov, 1981;

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Figure 1. Adult male *Chameleo jacksonii* from an introduced population in Nairobi. Photo by J. B. Losos.

Webb *et al.*, 2003). In the absence of other data, foraging mode could be a useful indicator of other organismal traits, possibly even predicting the effect an invasive species might have on an ecosystem (Phillips *et al.*, 2003; Watari *et al.*, 2008; Wiles *et al.*, 2003).

Chameleons have unusual morphological and behavioral traits (Bickel and Losos, 2002; Burrage, 1973; Losos *et al.*, 1993; Parcher, 1974; Peterson, 1984), possibly influencing how these predatory lizards gather food. Butler (2005), using behavioral data from a single species, *Bradypodion pumilum*, suggested chameleons be included in a third foraging class, "cruise forager," because of their unusual, slow-moving foraging behavior. The term "cruise forager" was first suggested by Regal (1978) as an intermediate stage between active and ambush foraging, "a species that moves, stops, and merely scans the environment, then moves, stops, and scans, and so on" (Regal, 1983, p. 114). In this study, we quantify a second chameleon species' foraging behavior, the Hawai'ian invasive *Chamaeleo jacksonii*. We make comparisons to *B. pumilum*

and other lizard species to investigate whether chameleons do exhibit a novel hunting strategy (Butler, 2005).

MATERIALS AND METHODS

Jackson's chameleon, *Chameleo jacksonii xantholophus* (Fig. 1), was originally introduced into Hawai'i in 1972 from Mt. Kenya, Kenya, as a result of the pet trade. This species has since reached the islands of Oahu, Maui, Hawai'i, and Kauai and is typically found in disturbed habitats (Eason *et al.*, 1988; McKeown, 1991; Waring, 1997).

We observed adult *C. jacksonii* individuals from 3 to 21 August 2001, in the countryside near the town of Makawao on the Hawai'ian island of Maui. *Chamaeleo jacksonii* were located using a haphazard search method only on sunny days and observed from the ground using a standard video recorder for approximately 30 min. Individuals were not disturbed before or during the observation. After the video data were gathered, we captured each subject when possible and noted sex, snout–vent length (SVL), and mass and measured habitat parameters such

TABLE 1. STATISTICAL TESTS, DESCRIPTIONS, AND RESULTS USED IN THIS ARTICLE.

Test Description	Test	Test Statistic	P
Mass vs. sex/age class in *C. jacksonii*	*F*-test	$F_{3,21} = 1.74$	0.19
SVL vs. sex/age class in *C. jacksonii*	*F*-test	$F_{3,22} = 1.74$	0.19
PTM vs. chameleon species	*F*-test	$F_{1,49} = 0.03$	0.9
MPM vs. chameleon species	*F*-test	$F_{1,49} = 6.01$	0.02*
MPM vs. PTM in *C. jacksonii*	linear regression	$MPM = 0.59 \times PTM + 0.08$, $r^2 = 0.50$	$\ll 0.01$*
MPM vs. PTM in *B. pumilum*	linear regression	$MPM = 0.49 \times PTM + 0.23$, $r^2 = 0.23$	0.02*
MPM vs. PTM	ANCOVA	$F_{1,48} = 25.0$	<0.01*
MPM vs. chameleon species	ANCOVA	$F_{1,48} = 8.95$	<0.01*
MPM vs. SVL in *C. jacksonii*	linear regression	$MPM = -0.22 \times SVL + 1.23$, $r^2 = 0.06$	0.3
PTM vs. SVL in *C. jacksonii*	linear regression	$PTM = -0.37 \times SVL + 1.90$, $r^2 = 0.14$	0.07
MPM vs. sex/age class in *C. jacksonii*	*F*-test	$F_{3,23} = 1.42$	0.3
PTM vs. sex/age class in *C. jacksonii*	*F*-test	$F_{3,23} = 1.05$	0.4
MPM vs. SVL in *B. pumilum*	linear regression	$MPM = -0.18 \times SVL + 1.07$, $r^2 = 0.03$	0.5
PTM vs. SVL in *B. pumilum*	linear regression	$PTM = 0.18 \times SVL - 0.52$, $r^2 = 0.04$	0.4
MPM vs. sex/age class in *B. pumilum*	*F*-test	$F_{2,21} = 3.21$	0.07
PTM vs. sex/age class in *B. pumilum*	*F*-test	$F_{2,21} = 1.90$	0.2
MPM and PTM in chameleons vs. active vs. ambush foragers	MANOVA	Wilk's lambda $F_{4,90} = 32.1$	$\ll 0.01$*
MPM and PTM in chameleons vs. active foragers	MANOVA	Wilk's lambda $F_{2,13} = 7.10$	<0.01*
MPM and PTM in chameleons vs. ambush foragers	MANOVA	Wilk's lambda $F_{2,32} = 29.3$	$\ll 0.01$*
MS and AS in active vs. ambush foragers	MANOVA	Wilk's lambda $F_{2,48} = 105$	$\ll 0.01$*
MS and AS in *C. jacksonii* vs. active vs. ambush foragers	MANOVA	Wilk's lambda $F_{4,96} = 49.5$	$\ll 0.01$*

*$P < 0.05$.

as perch height and diameter by climbing trees or using a long pole with calibrated markings. We then released the animal at the site of capture. To estimate movement distances, we used the animal's snout–vent length (SVL). Chameleons were marked with nontoxic paint to prevent observation of the same individual more than once.

We used the recorded videos to quantify each individual chameleon's foraging behaviors. We counted all behaviors (e.g., movements, position adjustments, displays, and eating events; see Butler, 2005) and noted the amount of time to complete each task. With these values, we calculated the number of moves the animals made per minute (MPM), percent time the animal spent moving (PTM), position adjustments per minute (PAPM), percent time adjusting position

(PTAP), and number of eating events per hour (EPH). Movements were defined as any event in which there was physical displacement of the animal's body. We used the video in conjunction with our habitat measurements to calculate two different measurements of speed: moving speed (MS) and mean or average speed (AS; see Cooper, 2007). Moving speed represents the speed of the animal while it was actually moving, analogous to instantaneous speed (distance moved, taken from habitat measurements, divided by the length of time required to complete the movement, calculated by counting frames in the videotapes). Mean speed was calculated by adding the entire distance moved during the observational period divided by the length of the observational period. These values were compared
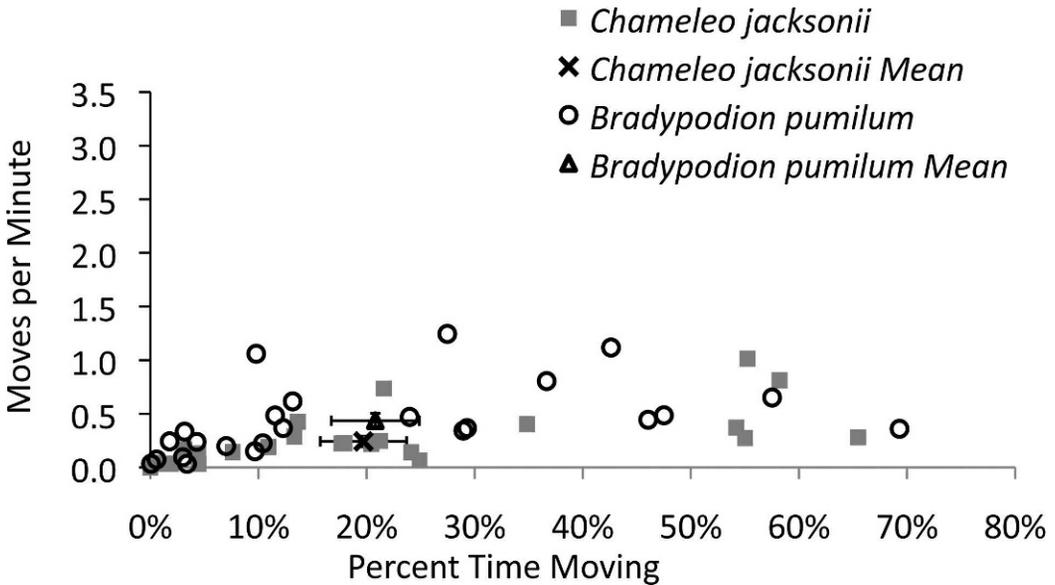
Figure 2.   Percent time moving (PTM) versus moves per minute (MPM) for *Bradypodion pumilum* (Butler, 2005) and *Chameleo jacksonii* (this study). Species $\bar{X} \pm 1$ SE. Error bars present on the Y-axis are obscured by point markers.

with data from Cooper's (2007) literature review of lizard speeds for 51 species. All variables were natural log or arcsine transformed for normality before statistical analyses. We compared our calculated behavior parameters to data from two previous studies (Butler, 2005; Cooper, 2007).

RESULTS

All values presented are means plus or minus standard errors. We collected data on 27 chameleons: 14 males, 12 females, and two juveniles with mean male SVL 106.5 ± 6.3 mm, mean mass 37.2 ± 7.1 g; mean female SVL 107.5 ± 6.6 mm, mean mass 43.9 ± 10.0 g; mean juvenile SVL 77 ± 1.0 mm, mean mass 12 ± 1.0 g. Neither mass nor SVL was dependent on sex/age class (Table 1). *Chamaeleo jacksonii* perched 4.5 ± 0.4 m off the ground on 2.42 ± 0.57 cm perches, adjusted position 0.22 ± 0.04 times per minute, spent 4.75 ± 0.99% of their time adjusting position, and ate 1.85 ± 0.53 times per hour. We did not observe any display events.

PTM and MPM values were similar between *C. jacksonii* (PTM = 19.7% ± 4.0%, MPM = 0.24 ± 0.05) and *B. pumilum* (PTM = 20.8% ± 4.1%, MPM = 0.44 ± 0.07, data from Butler, 2005; Fig. 2), although values varied greatly among individuals. *Chamaeleo jacksonii* did, however, move significantly less often than *B. pumilum* (Table 1). In both species, MPM was positively correlated with PTM (Table 1; species × PTM interaction term not significant, P = 0.65, and omitted from analysis). Neither MPM nor PTM was significantly dependent on SVL or sex/age class in both *C. jacksonii* and *B. pumilum* (Table 1).

Chameleons are distinct from a range of other active and ambush foraging lizard species both in regard to MPM and PTM (Fig. 3, Table 1; data from Butler, 2005). We also compared moving speed and mean
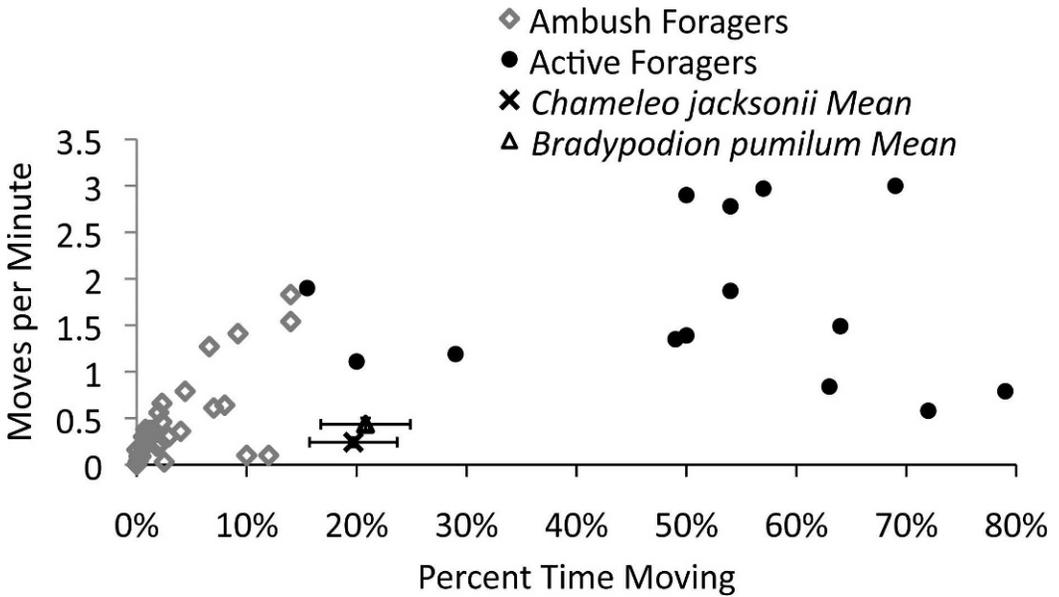
Figure 3. Percent time moving (PTM) versus Moves Per Minute (MPM) for a variety of lizard species including *Bradypodion pumilum* (Butler 2005) and *Chameleo jacksonii* (this study). Species $\bar{X} \pm 1$ SE. Error bars present on the *Y*-axis are obscured by point markers.

speed (see *Methods*) for *C. jacksonii* (MS = 0.33 ± 0.09 m/min, AS = 0.052 ± 0.01 m/min; Fig. 4) and found, in agreement with Cooper (2007), that active foragers display a slightly lower moving speed and much higher mean speed (Table 1). Again, chameleons seem to represent a foraging mode substantially different from the standard lizard foraging categories (Table 1).

DISCUSSION

Our data suggest that *C. jacksonii* exhibits a moderate percent time moving, low moves per minute, and a very slow locomotion speed. This combination of parameter values is rarely seen in other lizard species and is strikingly similar to data from the only other chameleon studied, *B. pumilum* (Butler, 2005). Although only two chameleon species have been evaluated, many lizard clades show little variation in foraging mode, which suggests that chameleons as a group might exhibit a unique foraging style (Perry, 2007). Our data support Butler's (2005) suggestion that chameleons be classified as cruise foragers. Interestingly, a second genus of lizards, *Chamaeleolis*, which lies phylogenetically with the *Anolis* clade and is only distantly related to chameleons (Townsend *et al.*, 2004), might exhibit similar behavior (Leal and Losos, 2000).

The morphology of chameleons is highly divergent from nearly all other species of lizards. This unique morphology may have facilitated a novel hunting strategy not used by other predators. Thus, one might expect chameleons to have distinct effects on prey behavior and their surrounding communities, a point to consider when evaluating native as well as introduced ecosystem interactions. More research is necessary to better understand the implications of chameleons' novel morphological and behavior-
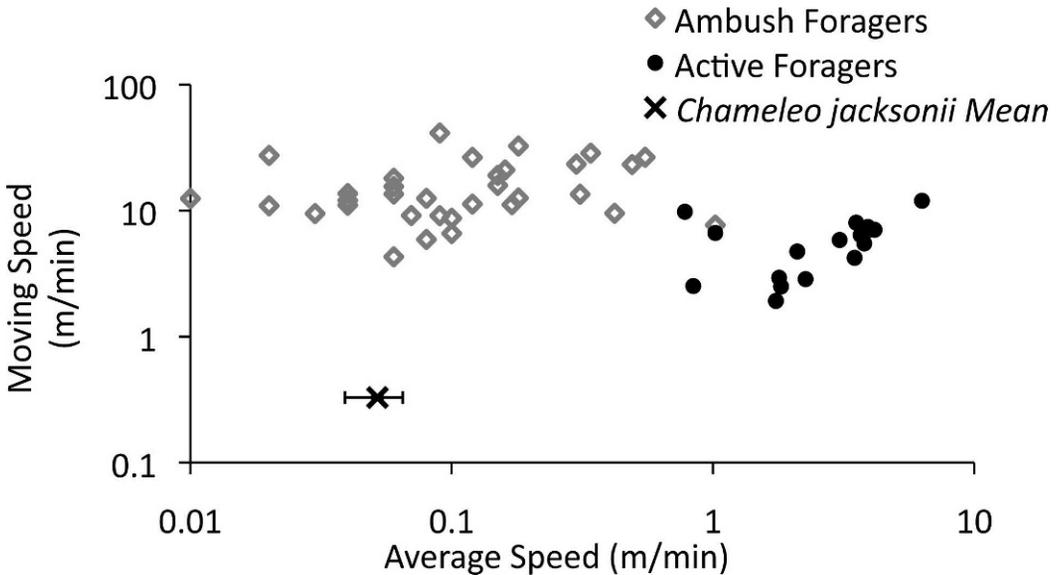
Figure 4.   Movement speed (AS vs. MS) for a set of lizard species (Cooper 2007) with the addition of *Chameleo jacksonii* (this study). Species $\bar{X} \pm 1$ SE. Error bars present on the *Y*-axis are obscured by point markers.

al adaptations, as well as the ramifications of chameleons' foraging mode on their surrounding community structure.

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