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Ecological Correlates of Small Territories and Intra-Seasonal Variation in the Social Context of Displays in Male Water Dragons, *Intellagama lesueurii*

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ABSTRACT.—**Size and location of territories have important fitness consequences for breeding males in many species, including lizards. Australian Water Dragons (*Intellagama lesueurii*) are an interesting study system in which to examine socio-ecological aspects of territory size and male behavior because, despite their large body size, these lizards form dense aggregations within urban riparian habitats. In one such population, we found that males defended territories smaller than have been reported for most other large lizards. Surprisingly, smaller males defended larger territories, but larger territories did not increase access to females. Instead, territory size was negatively correlated with conspecific density, including females, which in turn was highest near a creek that provided abundant prey and refuges. That is, territories were smaller in sites offering more resources for reproduction, feeding, and predator evasion. The relative proportion of displays males gave during contests with rivals did not vary within the reproductive season. However, male travel and the context of stereotypical head displays showed a surprising pattern of seasonal variation. As the season progressed, males increased the proportion of displays to females, but decreased the proportion of undirected territorial advertisement displays. Because Water Dragons are long-lived and philopatric, increased display during interactions with postbreeding females may enhance mating opportunities in future reproductive seasons.**

Territorial behavior is expected to evolve when the benefits of controlling access to defended areas exceed the cumulative costs (Davies and Houston, 1984; Stamps, 1994; Moore et al., 2014). Costs of male spatial defense include time and energy required for patrolling boundaries and repelling same-sex competitors, increased vulnerability to predators while engaging rivals, and lost foraging opportunities during defensive activities. Male fitness is typically limited by the number of mates (Trivers, 1972), and access to females is a common fitness benefit that males derive by defending territories (Stamps, 1994; Baird and York, 2021). When breeding females are moderately clumped (Emlen and Oring, 1977), males may be able to defend multiple mates (polygyny), and increasing the size of territories may allow males to encompass more female home ranges (Hixon, 1987; Baird, 1988). Therefore, territory area is commonly measured in studies of mating ecology, including those on lizards.

Previous studies have suggested that long-lived (ca. 20 y) Australian Water Dragons (*Intellagama lesueurii*, formerly *Physignathus*, Agamidae; Gray, 1831) provide an interesting system in which to investigate the social ecology of breeding territory defense. Although *I. lesueurii* is the largest (up to 1 kg) Australian agamid, both natural and urban populations thrive in small patches of riparian habitat (Thompson, 1993; Baird et al., 2012; Baxter-Gilbert, 2018). At our study site, female home ranges were very small and highly overlapping (Baird et al., 2021), suggesting that males might access numerous mates by only defending small areas. Our first objective, therefore, was to use data that we recorded previously (Baird et al., 2012, 2020) to compare the relative size of male Water Dragon territories with the relative size of areas used by males in other large lizard species (see similarly Baird et al., 2021).

In our study population, larger males with larger heads had higher resource holding power (= RHP, sensu Parker, 1974), which enabled them to defend territories against numerous nonterritorial male rivals (Baird et al., 2020). The relative importance of overt aggression versus advertisement displays in territory maintenance also depended on the extent to which the intervening vegetation blocked visual signals by males, and the small home ranges of females were crowded along the shoreline of a creek bisecting our study site (Baird et al., 2012, 2013, 2014, 2020). Therefore, our second objective was to test the extent to which variation in territory area among male Water Dragons was linked with male morphometry as well as ecological factors that may influence the benefits and costs of territory defense.

Lastly, we explored how territorial Water Dragon males balanced the competing demands of defense with their ability to form current and future mating relationships (Clutton-Brock et al., 1979; Pryke, 1979; Nolet and Rosell, 1994; Eason and Switzer, 2004) by determining within-season variation in the social context of male displays. One possible within-season pattern of male social behavior is to invest most heavily in courtship displays early in the season when females are vittellogenic, but then switch to invest in territory defense and patrol postmating to increase the chances of re-establishing territories in the future (Baird et al., 2001). The high level of multiple paternity and potential for postcopulatory sperm selection in female Water Dragons (Frère et al., 2015), however, may select for the opposite within-season pattern. That is, males may display to females late in the season if this tactic enhances mating relationships with particular females into the following season, and/or female Water Dragons use stored sperm to fertilize eggs (as is common in many other lizards; Uller and Olsson, 2008).

METHODS AND MATERIALS

Study Species and General Methods.—Water Dragons are diurnal, semiaquatic lizards that occur throughout New South Wales and southern Queensland, Australia, in natural and urban riparian habitats (Littleford-Colquhoun et al., 2017; Wilson and Swan, 2017; Baxter-Gilbert, 2018). Diet of Water Dragons consists of arthropods, fish, other lizards (small scincids, juvenile conspecifics), and occasionally small mammals (MacKay, 1959; Wilson and

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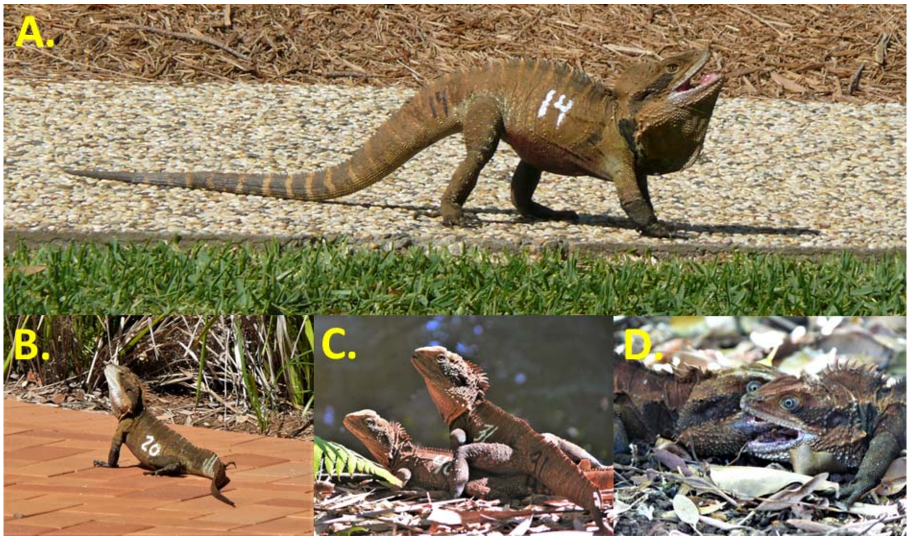

FIG. 1. Male Water Dragons performing a full show and a head-up while distant from conspecifics (A, B), a male (top) and female engaged in courtship (C), and two males engaged in an aggressive contest (D).

Knowles, 1992; Meek et al., 2001). Our study population was located on the grounds of the Flynn's Beach Resort (−31.4461°S, 152.9272°E, datum WGS84, 22 m elevation), Port Macquarie, New South Wales, where all wildlife was protected (Baird et al., 2012). At our study site, lizards used the natural riparian habitat on both sides of a 0.2-km stretch of Wright's Creek, but also the cultivated lawns, plant beds, cement, tile, and wood decks of the resort (Baird et al., 2020). To map the 0.88-ha study site, in September 2009 we recorded distance (±2.0 m) and compass measurements among at least five human-constructed landmarks (e.g., concrete and wooden walkways, foot bridges, fence and light posts), large trees, and the creek shoreline. The human-constructed landmarks were intact when we repeated the study in 2016, except that some trees had been cut down so that only the stumps were present. We expanded our study area by 15% in 2016 and mapped this additional area using the same methods (Baird et al., 2020).

We captured lizards using a noose on the end of a pole, marked them permanently by clipping the ends of three digits, and numbered each lizard for identification from a distance. Mature male Water Dragons develop a red–orange–black patch on the ventral side of the torso that is revealed only during stereotypical displays to signal rivals (Baird et al., 2013). To avoid potential interference with signaling, we painted numbers on each side of the dorsal torso (white nail polish), and each side of the tail base (black felt pen). Both areas were uniformly brown in both sexes and were visible when lizards were not displaying (Fig. 1A–C). We observed marked lizards from ≥10 m, which did not disturb behavior. At first capture (15–25 September 2009, 12–21 September 2016), we measured male snout–vent length (SVL; ±1 mm), body mass (±5 g), and body dimensions (see Baird et al., 2012, 2020 for detailed methods). Maturity in males was determined by hemipene eversion and dimorphic ventral coloration (Baird et al., 2012, 2020). We regressed ln mass (g) on ln SVL (mm) and used the regression residuals as our estimates of male body condition (Warner et al., 2008; Cox et al., 2010).

Interspecific Comparison of Standardized Territory or Home Range Area.—We used the minimum convex polygon (Rose, 1982; Stone and Baird, 2002) technique to map the size and location of territories of male Water Dragons (2009, $n = 14$, 2016, $n = 10$; $\bar{x}$ SVL = 251 mm ± 2.1 SE). We recorded the locations of all emergent lizards during 58 censuses from 24 September to 26 November 2009, and 74 censuses from 12 September to 30 November 2016, plus the beginning and ending points of focal observations (described below) on males. For the present study, we only used data recorded during unmanipulated baseline conditions to estimate male territory area. Area estimates were based on a minimum of 70 sightings recorded during censuses plus focal observations ($\bar{x}$ ± 1.0 SE, 2009 = 87.1 ± 2.1; 2016 = 75.0 ± 1.2).

For interspecific comparisons, we used published data on the areas used by males in other large lizard species (male SVL ≥ 15.5 cm) because the amount of space used by individual lizards generally increases with body size (Perry and Garland, 2002). Some of the studies that we included in our comparison also recorded behavioral observations indicating territory defense whereas others did not. Therefore, hereafter we refer to values determined for males of other species as "areas." The available sample included 10 carnivorous and 10 herbivorous taxa representing six family-level clades. Hence, we did not control for effects of phylogeny. Altogether, we used data from 19 studies summarized by Perry and Garland (2002) plus 7 more recent studies for a total of 26 values on 19 diurnal species. All of these studies used the convex polygon method to estimate home range area for ≥4 males.

Correlates of Territory Area.—We used Principal Component Analysis (hereafter, PCA) to summarize variation among males and their territories, and then univariate regressions to explore relationships between areas of territories defended for ≥1 mo (2009, $n = 14$; 2016, $n = 10$) and PC Factors that explained ≥10% of total variation among males. In 2009, territorial males were larger than mature nonterritorial males, and 2009 males also had relatively larger heads than in 2016 when levels of intrasexual aggression were diminished (Baird et al., 2012, 2020). Therefore, we first used PCA to summarize intercorrelated morphological attributes of territorial males that might influence their RHP. We included SVL, body mass, head length, head height, head width, and length of front and hind legs (see Baird et al., 2012, 2020) in this PCA of morphometric variables. We then used least-squares univariate regression to examine the extent to which PC factors were significant predictors of territory area (m^2), which we log base-10–transformed to meet requirements for parametric statistics.

We used a second PCA to summarize variation in 5 socio-ecological variables that may influence the benefits and costs of defending space. Included were densities of rival males and resident females, male body condition, length of shoreline that intersected territories, and maximum horizontal visibility at ground level from territory centers. Rival male and female densities (lizards/m^2) were calculated separately as the number of lizards whose home ranges bordered or partially overlapped male territories. We included density of rival males because it may influence costs of defense, and density of females and length of intersecting shoreline because these likely reflect benefits of territory defense (i.e., mating opportunities and access to aquatic refuges from predators). We included horizontal visibility because we previously showed that the degree to which intervening vegetation obstructed visibility influenced use of visual signals by males (Baird et al., 2020). Lastly, differences between territorial and nonterritorial males suggested that body condition may reflect male RHP (Baird et al., 2012), so we included it in our second PCA. We used residuals from a linear regression of ln SVL on ln total body mass ($F_{1,23} = 31{,}837$, $P < 0.0001$, $R^2 = 0.992$) to estimate male body condition, similar to studies of other lizards with body shapes like that of Water Dragons (López and Martín, 2002; Warner et al., 2008, Cox et al., 2010). As with our PCA of morphometric variables, we used univariate regression to examine the extent to which PC factors were significant predictors of log-transformed territory area.

Within-Season Variation in the Social Context of Male Display.—We recorded focal observations (sensu Altmann, 1974) to test how the social context of male displays varied from the beginning to the end of the reproductive season in 2016. From 17 September through 28 November, we recorded 20–40 min of focal observations/territorial male/day at least every 3 d in the 8 males that defended territories throughout this entire period. Daily observations were recorded in random order from 0800–1600 h when air temperatures were 23–30°C. To avoid any effects of one-day removal experiments ($n = 6$) conducted in 2016, we did not include observations recorded any less than 3 d after the end of experiments. Although 10 males defended territories on our study site in 2016 (Baird et al., 2020), 2 territory owners were spontaneously displaced by nonterritorial rivals. Therefore, we limited our sample to the 8 males that held their same territories throughout the entire reproductive season (September–November).

For each focal observation session, we traced the travel path of subject males on maps and recorded the locations and social contexts of all male displays. Most displays involved stereotypical movements of the head and torso (described in Baird et al., 2012, 2020; Fig. 1A, 1B). Broadcast displays were performed when subject males were farther than 1.0 m from a conspecific and not moving toward it (Baird et al., 2020). Courtship displays were those given when males were approaching females that responded by lowering their heads and arching the proximal tail upward, or while the two lizards remained within one body length of each other making physical contact (Fig. 1C). Displays given during contests with rivals were those when males were moving toward or within 1.0 m of a rival male that was also displaying, approaching, fleeing, or fighting back (Fig. 1D). For each observation day, we tallied the total displays performed and the proportion given during each social context (broadcast, contest, courtship).

We used generalized linear mixed models for analyses using the lme4 package in Program R version 4.0.3 (R Core Team, 2021). Observation date was the predictor variable. Response variables were travel rate (m/min) analyzed using a Gaussian family distribution, the proportions of total displays that were broadcast while distant from conspecifics, and displays given during male–male contests or during courtship interactions, all analyzed using a binomial family distribution, logit link function. Repeated observations on multiple males were controlled for by incorporating male identity as a random effect in all models. We report results for observation date as standardized effects (β) with associated 95% confidence intervals (CI) and *P*-values. Results were considered statistically significant ($P < 0.05$) if the 95% CI did not overlap 1.0.

RESULTS

Interspecific Comparison of Male Space Use.—Territories used by male Water Dragons ($\bar{x} = 682$ m^2, SE = 92.0, range = 163–1,703) were smaller ($z_{23,25} = 5.21$, $P < 0.0001$) than were the areas used by males in 26 other species of lizards of large body sizes (≥ 15.5 cm SVL; Table 1). However, average body size of these 20 large lizards also exceeded that of males in our population ($z_{23,25} = 3.09$, $P = 0.002$) because the sample included several very large species, especially varanids (Table 1). When we limited the heterospecific sample to species ($n = 14$) that were ≤ 40.0 cm SVL ($\bar{x} = 26.2$, SE = 2.0, range = 15.5–37.4), average size of Water Dragon territories was still only 0.7% ($z_{13,23} = 4.10$, $P < 0.0001$) of the mean area used by this sample of smaller species.

Correlates of Territory Area.—PC analysis of morphometric variables revealed three factors that explained $\geq 10\%$ of the variance among territorial males. PC1 accounted for most (55.5%) of the variance, whereas PC2 and PC3 explained 17.8 and 11.1% of the variance respectively (Table 2). SVL and all three head dimensions loaded highest and negatively on PC1. Body mass and hindleg length loaded highest on PC2, with a positive loading for mass and a negative loading for hindleg length. Only front leg length loaded highest (negatively) on PC3. Regression analysis revealed a significant positive relationship between PC1 scores and territory size ($F_{1,23} = 6.12$, $P = 0.022$) that explained 22% of the variance in size of areas defended by males (Fig. 2). By contrast, neither PC2 ($F_{1,23} = 1.76$, $P = 0.199$, $R^2 = 0.07$) nor PC3 ($F_{1,23} = 0.20$, $P = 0.66$, $R^2 = 0.01$) scores were significant predictors of male territory area.

PC analysis of socio-ecological variables revealed four factors that collectively explained 95.4% of the total variance in ecological parameters characterizing male territories, but the pattern of positive and negative loadings was complex (Table 3). Density of both rival males and females loaded highest and positively on PC1 (40.4% of variance), but the positive loading for female density on PC4 (12.3% of the variance) was nearly as high. Body condition and horizontal visibility loaded highest and positively on PC2, but the positive loading for visibility was also high on PC3 (Table 3). The amount of shoreline alone loaded highest and negatively on PC3, but it also had a relatively high negative loading on PC1 and a high positive loading on PC4. The only statistically significant relationship with male territory area was a strong negative association ($F_{1,23} = 101.4$, $P < 0.001$) with PC1 scores (= density of conspecifics), which explained 82% of the variance in territory size (Fig. 3). By contrast, relationships between male scores for PC2–PC4 and territory area were not statistically significant ($F_{1,23} = 0.03$–0.19, $P = 0.67$–0.85, $R^2 = 0.002$–0.009).

TABLE 1. Comparison of amount of space used by adult male Water Dragons to that used by 19 other large lizard species ($\bar{x}$ adult male snout–vent length [SVL] $\geq$ 15.5 cm). Diet codes: C = carnivores, H = herbivores.

Lizard taxon	Source	Diet	Area (m^2)	SVL (cm)
Agamidae				
Intellagama lesueurii	this study	C	690	25.0
Chlamydosaurus kingii	Griffiths, 1999	C	18,100	24.0
Uromastyx aegyptia	Bouskila, unpubl. data	H	33,733	37.3
Helodermatidae				
Heloderma suspectum	Beck and Lowe, 1991	C	494,000	32.7
	Kwiatkowski et al., 2008		277,500	27.3
Iguanidae				
Conolophus pallidus	Christian and Tracy, 1985	H	8,050	62.6
	Christian et al., 1986		6,450	62.6
Brachylophus vitiensis	Morrison et al., 2013	H	64	20.6
Cyclura cornuta stejnegeri	Pérez-Buitrago et al., 2010	H	4,200	54.2
C. cychlura cychlura	Knapp and Owens, 2005	H	110,800	47.7
C. lewisi	Goodman et al., 2005	H	143,000	40.7
C. pinguis	Mitchell, 1999	H	4,000	49.0
	Carey, 1975		546	53.4
C. rileyi rileyi	Cyril, 2001	H	1,076	26.6
Iguana iguana	Dugan, 1982	H	2,200	31.0
	Rand et al., 1989		14,144	37.4
Sauromalus ater	Johnson, 1965	H	5,700	15.5
	Nagy, 1973		2,000	16.1
	Berry, 1974		19,000	20.0
Lacertidae				
Timon lepidus	Castilla and Bauwens, 1982	C	1,324	20.0
Scincidae				
Tiliqua rugosa	Bull and Freake, 1999	C	51,760	34.0
Varanidae				
Varanus albigularis	Phillips, 1995	C	18,300,000	77.0
V. bengalensis	Auffenberg et al., 1991	C	104,000	61.0
V. griseus	Stanner and Mendelssohn, 1987	C	984,000	40.2
	Tsellarius et al., 1995	C	255,600	45.8
V. mertensi	Mayes, 2006	C	77,761	43.1
V. tristis	Thompson et al., 1999	C	400,000	25.5

Within-Season Variation in Male Behavior.—Both the rate of male travel ($\beta = -0.24$, 95% CI = -0.35 to -0.13, $P < 0.00001$) and the proportion of all displays that were given while distant from conspecifics decreased as the reproductive season progressed ($\beta = -0.39$, 95% CI = -0.50 to -0.28, $P < 0.00001$), whereas there was no significant effect of observation date on the proportion of displays given during male–male contests ($\beta = 1.02$, 95% CI = 0.52–2.00, $P = 0.95$). In marked contrast, the proportion of displays given by males while interacting with females increased as the reproductive season progressed ($\beta = 2.97$, 95% CI = 2.07–4.25, $P < 0.00001$).

DISCUSSION

Male Water Dragons defended areas that were smaller than all but 2 of 19 other large lizard species. Male Fijian Crested Iguanas (*Brachylophus vitiensis*) had areas that were less than one-half as large as that of Water Dragons, probably because lizard density was extremely high in this island population (Morrison et al., 2013). Areas used by male Rock Iguanas (*Cyclura pinguis*) in another island population were also smaller than territories of Water Dragons. The latter population was not particularly dense, but like Water Dragons that typically remained close to aquatic refuges, Rock Iguanas were restricted to limestone outcrops where they took refuge in crevices (Carey, 1975). We cannot rule out the possibility that male Water

TABLE 2. Loadings of seven morphometric variables in male Water Dragon territory owners on PC factors that explained $\geq$10% of the total observed variation.

Variable	PC1 (55.5%)	PC2 (17.8%)	PC3 (11.1%)
Snout–vent length	−0.451	−0.085	−0.055
Mass	−0.298	0.587	−0.174
Head length	−0.443	0.009	0.219
Head height	−0.426	0.196	0.078
Head width	−0.471	0.044	0.016
Hind leg length	−0.243	−0.683	0.369
Front leg length	−0.243	−0.376	−0.867

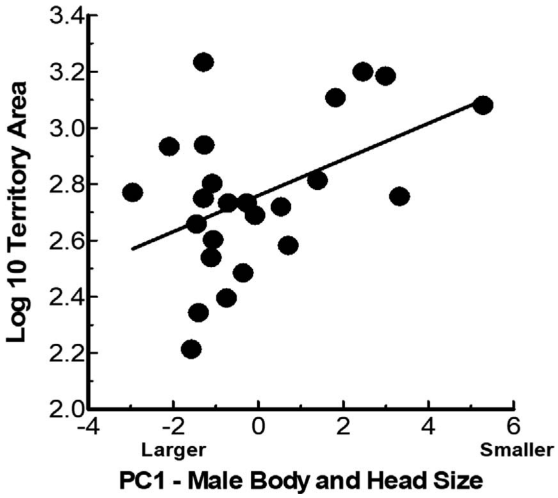

FIG. 2. Territory area (m^2) of male Water Dragons graphed against PC1 scores (snout–vent length [SVL] and head size).

TABLE 3. Loadings of five variables describing ecological attributes of Water Dragon territories and their male owners on PC factors that explained ≥10% of the total observed variation.

Variable	PC1 (40.4%)	PC2 (27.4%)	PC3 (15.3%)	PC4 (12.3%)
Density of rival males	0.644	0.038	−0.228	0.014
Density of females	0.567	0.254	−0.078	0.553
Shoreline length	−0.488	0.142	−0.604	0.572
Horizontal visibility	−0.160	0.654	0.629	0.248
Body condition	0.007	0.697	−0.427	−0.552

Dragon territories were smaller than areas used by most large lizards because we limited observations to the reproductive season. Water Dragon males may expand space use outside of the reproductive season, especially if waterways allow movement without increasing vulnerability to predators.

Some theoretical models predict that breeding males should maximize size of defended areas to increase reproductive success (Hixon, 1987), and the number of females accessed does increase with male territory area in some systems (Baird, 1988; Vanpe et al., 2009). In our examination of the relationship between male morphology and territory size, regression of territory area versus PC1 scores revealed a positive relationship. However, all the highest loadings on PC1 (SVL, three head dimensions) were negative (Table 2); therefore, this means that smaller males (those with more positive PC1 scores) had larger territories (Fig. 2). Assuming growth continues as Water Dragon males age, smaller males may have been younger and perhaps more vigorous. Contests between territory owners and challengers were sometimes long and physically strenuous (Baird et al., 2012), hence vigor may indeed influence the ability of males to successfully hold larger territories in this population.

By contrast, in our PCA of ecological variables the highest loadings on PC1 (female and male density) were positive (Table 3), with male territory area decreasing as scores on this axis increased (Fig. 3). Therefore, despite competitive pressure from more male rivals, defending territories along the creek where females aggregated (Baird et al., 2021) allowed males to access numerous potential mates. Territories along the shoreline would also provide abundant prey, as well as aquatic refuges from predators (e.g., monitor lizards), excessive heat, and darkness (Courtice, 1981; Baxter-Gilbert, 2018; Baird et al., 2021), all suggesting that the riparian zone was high quality habitat in which to establish territories.

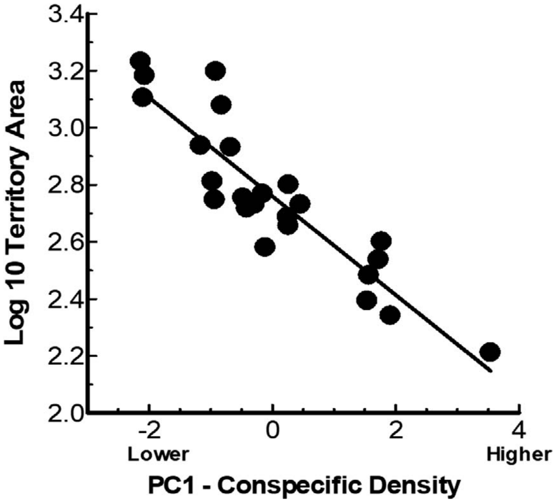

FIG. 3. Territory area (m^2) of male Water Dragons graphed against PC1 scores (conspecific density).

Although in our analysis of socio-ecological variables PC1 was the only factor that significantly predicted territory area, combinations of the highest (or nearly as high) positive and negative loadings on all four PC axes suggest other possible trade-offs between access to beneficial resources and defense costs. For example, high positive loadings for body condition and horizontal visibility on PC2 may indicate that males in better condition occupied territories where visibility was higher. Displaying is less costly than fighting; therefore, males on territories with higher visibility may save energy, which in turn improves their condition. Results showing that territory owners relied less on direct confrontation and more on visual displays when removal of some trees enhanced transmission of visual signals (Baird et al., 2020) is consistent with this hypothesis.

A high negative loading for shoreline length together with a relatively high positive value for visibility on PC3 may suggest that territories having high visibility had less shoreline. The pattern of positive and negative loadings on PC1 and PC4 is also intriguing. Female density loaded high and positive on both PC1 and PC4, whereas shoreline had a high negative loading on PC1 but a high positive value on PC4. Body condition also loaded high and negative on PC4. The combined loadings may suggest that defending territories where females are dense but shoreline is diminished is costly enough to reduce male body condition. The two males that controlled territories not intersecting the creek (see below) appear informative about these possible trade-offs. In each case, horizontal visibility was higher whereas body condition was lower relative to the mean values for all territories and males, which are each consistent with expectations for these proposed trade-offs.

Social polygyny based on male defense of resources (Deslippe and M'Closkey, 1991; Calsbeek and Sinervo, 2002; Kwiatkowski and Sullivan, 2002), or direct defense of females (M'Closkey et al., 1987; Jenssen et al., 2001; Baird and Leibold, 2023) have both been documented in lizards. In our population, even though mature nonterritorial males were abundant and all territories shared borders with 1–4 territorial neighbors, territory owners monopolized most of the social interactions with resident females (Baird et al., 2012, 2020). All but two territories intersected the creek where resources important to females (refuge and prey) were abundant. The two territories surrounded terrestrial refuges used by several females—a crawlspace beneath an abandoned building, and a large pile of dead banana-tree branches. Clearly, male polygyny in this population is based on defense of habitat containing refuges (resource defense; sensu Emlen and Oring, 1977). Crowding into the riparian zone, however, may allow both females and males to mate with multiple partners (polygynandry) like the genetic mating system revealed by parentage studies in another dense urban Water Dragon population (Frère et al., 2015).

In our relatively small sample, travel and the proportion of displays broadcast when males were distant from conspecifics decreased toward the end of the reproductive season, whereas displays to females increased markedly. Intrasexual contests were rare relative to interactions with females in this and a previous study (Baird et al., 2012), and the proportion of displays during intrasexual contests did not vary seasonally. Within-season variation in the behavior of male territory owners has largely been neglected in vertebrates including lizards, with most studies being limited to comparisons of males during breeding and nonbreeding periods (Ruby, 1978; Rhodda, 1992; Demko and Mennill, 2018). Whether or not adults disperse following breeding may have important effects on within-season variation in male behavior (Baird et al., 2001). If adults emigrate when breeding is finished (as in many birds), establishing territories the following season may require males to display frequently during contests among the newly settled cohort of males, whereas bonding with mates can be delayed because females typically arrive later (Baird et al., 2001; Yasukawa and Searcy, 2020).

The expected within-season pattern of male behavior is different in lizards than in birds because dispersal by lizards is more limited and individuals maintain philopatry to the same breeding sites between seasons (Baird et al., 2001; Fox et al., 2003). Why might it be advantageous for territorial Water Dragon males to increase the proportion of their social displays toward females late in the reproductive season after the last eggs produced that season have already been fertilized? One possibility is that frequent display while interacting with females as seasons end might promote mating opportunities in subsequent seasons. Water Dragons are long-lived (ca. 14–20 y; Thompson, 1993; Baxter-Gilbert, 2018), and some females in our population displayed long-term philopatry (Baird et al., 2020, 2021). Frequent late-season advertisement to resident females, therefore, may increase a male's mating success in the following season (see Koenig et al. 2001 for similar speculation for the large scincid lizard *Tiliqua scincoides*). It is also possible that female Water Dragons store sperm received during November copulations to fertilize eggs produced in the following spring. Sperm storage has not been demonstrated in *I. lesueurii*, but it occurs in at least two other agamids (Kast, 2007; Uller et al., 2013). Either possibility could increase both male and female lifetime fitness, if male Water Dragons that successfully hold territories throughout the reproductive season possess heritable traits that promote offspring fitness.

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