Behavioral Interactions for Food among Two Clones of Parthenogenetic Lepidodactylus lugubris and Sexually Reproducing Hemidactylus frenatus Geckos

Authors: Murakami, Yuki, and Hayashi, Fumio

Source: Current Herpetology, 37(2) : 124-132

Published By: The Herpetological Society of Japan

URL: https://doi.org/10.5358/hsj.37.124

Current Herpetology 37(2): 124–132, August 2018
© 2018 by The Herpetological Society of Japan
doi 10.5358/hsj.37.124

Behavioral Interactions for Food among Two Clones of Parthenogenetic *Lepidodactylus lugubris* and Sexually Reproducing *Hemidactylus frenatus* Geckos

YUKI MURAKAMI* AND FUMIO HAYASHI

Department of Biology, Tokyo Metropolitan University, Minamiosawa 1–1, Hachioji,
Tokyo 192–0397, JAPAN

Abstract: *Lepidodactylus lugubris* is an all-female parthenogenetic gecko. This gecko consists of diploid and triploid clones in the tropical and subtropical regions, and Clones A (diploid) and C (triploid) cohabit most islands in Ogasawara, Japan. On some Ogasawara islands, another cosmopolitan, but sexually reproductive, gecko *Hemidactylus frenatus* coexists with *L. lugubris*. This situation offers a unique opportunity to examine interactions not only between asexual female clones of *L. lugubris* but also between *L. lugubris* and both sexes of *H. frenatus*. We induced behavioral contests for food in small laboratory enclosures between two individuals of different clone, sex, and species combinations. Clone C interacted with other individuals less frequently and had a lower success in feeding the prey than Clone A and both sexes of *H. frenatus*. Clone C also showed few aggressive behaviors such as arches, growls, bites, and lunges, and never wrestled with other individuals. This interactive tendency of Clone C helps explain the microdistribution patterns of these sympatric geckos in the field.

Key words: Clonal diversity; Interference competition; Microhabitat shift; Ogasawara; Parthenogenesis

INTRODUCTION

Most vertebrates reproduce sexually, but some do asexually (Vrijenhoek et al., 1989; Schön et al., 2009; Avise, 2015). Parthenogenesis is an asexual reproductive mode that usually produces clonal offspring. However, genetically distinct multiple clones are known in several species of all-female parthenogenetic vertebrates (Vrijenhoek, 1984, 1989). In this case, ecological differentiation between the clones is necessary for them to co-exist in narrow habitats such as islands because overlap of their niches intensifies interclonal competition (Vrijenhoek, 1984, 1989). Competition occurs chiefly through exploitation and/or interference processes (Case and Gilpin, 1974).

Lizards include unexpectedly high numbers of asexual (parthenogenetic) all-female species (Cole, 1984; Kearney et al., 2009). Two parthenogenetic clones of the lizard *Cnemidophorus laredoensis* (LAR-A and -B) and their sexually reproducing relative *C. gularis*, overlap extensively in three niche

---

* Corresponding author. Tel: +81–042–677–2586; Fax: +81–042–677–2559;
E-mail address: ymurakami9406@yahoo.co.jp

dimensions including daily activity period, microhabitat use, and diet breadth; therefore, competition is expected to be intensive between these two species (Paulissen, 2001). In this genus, sexually reproducing *C. sexlineatus* (particularly the male) is more aggressive than three parthenogenetic congeners: diploid *C. tesselatus*, triploid *C. tesselatus*, and diploid *C. neomexicanus* (Leuck, 1985). Aggressiveness is also different between two local populations (probably the different clones) of *C. uniparens* (Grassman et al., 1991). Thus, interference competition may be severe among these sympatric sexually reproducting and parthenogenetic *Cnemidophorus* species.

Lepidodactylus lugubris is an all-female parthenogenetic gecko widespread over the Indian and Pacific Ocean islands and continental Asia and America (Moritz et al., 1993; Radtkey et al., 1995; Ineich, 1999; Yamashiro et al., 2000; Bosch and Páez, 2017; Señaris et al., 2017). Multiple clones have been identified genetically and morphologically, and several clones coexist on several Pacific islands (Ineich, 1988; Ineich and Ota, 1992; Hanley et al., 1994; Radtkey et al., 1995, 1996; Yamashiro et al., 2000). Inter-clonal differences of parthenogenetic *L. lugubris* in spatial distribution may be due to preferred temperatures of each clone, and this may promote their coexistence on small islands (Bolger and Case, 1994). On the other hand, individuals of *L. lugubris* are known to interact behaviorally towards each other in the field and laboratory conditions (Brown et al., 1991; Bolger and Case, 1992; Petren and Case, 1996; Short and Petren, 2008). There are no significant differences in the frequency of behavioral interactions between Clones A and B individuals (Bolger and Case, 1992). However, Clone A initiates foraging faster and consumes more insects than Clone B, and the latter is more active but shyer than the former (Short and Petren, 2008).

In the Ogasawara Islands, Japan, another clone, Clone C, often coexists with Clone A, but the microdistribution patterns differ between these two clones (Murakami et al., 2015; Murakami, 2017). The habitats of Clone A bias towards artificial environments such as house walls, electric poles, and road guardrails, whereas those of Clone C are mainly in natural areas such as forests, rock crevices, grasslands, and beaches. On the Ogasawara Islands, a sexually reproducing gecko, *Hemidactylus frenatus*, is also distributed in some islands (Murakami et al., 2015). This gecko has a wide distribution range in tropical and subtropical oceanic regions (Weterings and Vetter, 2018) and co-exists with *L. lugubris*, both of which are often found in the human habitats (Bolger and Case, 1992; Moritz et al., 1993). However, the competitive displacement by *H. frenatus* of an asexual resident gecko has also been documented over a wide geographic area, and the mechanism of competition was partly due to the behavioral dominance of *H. frenatus* over smaller *L. lugubris* in areas near concentrated food (Petren et al., 1993).

In the present study, we observed behavioral interactions between combinations of two individuals of Clones A and C of *L. lugubris*, and males and females of *H. frenatus*, by inducing behavioral contests for food in a small laboratory enclosure. This is the first description of behavioral interactions of Clone C with other clones and species. We discussed how their interactive tendency could help to understand the microdistribution patterns of these sympatric geckos in nature.

MATERIALS AND METHODS

A total of 111 females of Clone A and 92 females of Clone C of *L. lugubris* and 67 males and 68 females of *H. frenatus* were collected on Chichijima in July and August of two years, 2016 and 2017. In addition, 10 females of Clone C were collected on Mukojima in July 2017. Snout to vent length (SVL) of all captured individuals were measured to the nearest 0.1 mm, and the state of their tail (intact or regenerated tail) was recorded. Clone types of *L. lugubris* were identified by

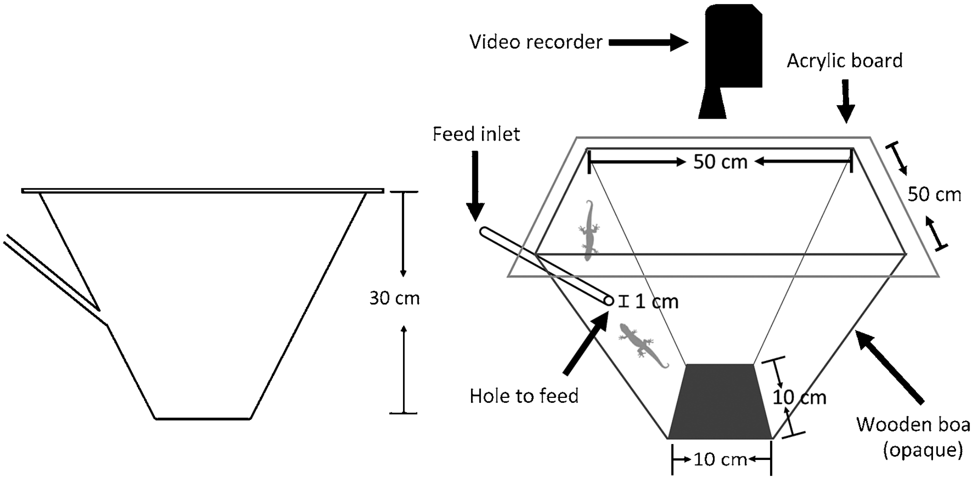

FIG. 1. Schematic drawing of the experimental enclosure for observation of interactions between two individuals of Clones A and C of *Lepidodactylus lugubris* and male and female *Hemidactylus frenatus*. For the methods of observation, see the text.

their dorsal color patterns (Ineich, 1999).

In the feeding experiments, we used five enclosures made with wooden boards, in which one small hole opened on one side of walls (Fig. 1). Geckos to use for the experiments were collected in the field before 7 to 15 h of video recording. They were kept together in one of the five enclosures to allow them move around within it. In darkness, two individuals selected from Clones A and C of *L. lugubris* and male and female *H. frenatus* (hereafter written as Clone A, Clone C, H-M, and H-F, respectively) were put into the empty enclosure, and the top of the enclosure was covered with a transparent acrylic board (Fig. 1). The behavior of the geckos was recorded using infrared sensitive function of the video camera (SONY FDR-AX55 or SONY DCRA-C160, Tokyo, Japan). After starting the video recording, one live small-sized mealworm (larvae in 12 to 16 mm in length of the beetle *Tenebrio molitor* Linnaeus, 1758) was thrown through the narrow pipe which opens at the enclosure wall. The minimum distance between the tip of the gecko's snout and the body edge of the mealworm were measured as the distance to food. We defined "contests" as feeding of a given prey animal with some aggressive behaviors between the two individuals, using the five aggressive behavioral categories by Dame and Petren (2006): arches (warping body), lunges, growls, bites, and wrestles. Therefore, we judged as no contest when one of the individuals consumed the given prey without these behavioral interactions. Individuals that fed the mealworm were judged as winners. This feeding trial using the single mealworm (a "round" hereafter) was repeated three times for the same pair, and each round continued until the mealworm was eaten by either individual. The mealworm was always eaten within 1 h. After the experiments, geckos were moved to another cage before releasing them at the capture sites in the next morning. No individuals were used twice. To prevent recapture, we changed the collecting sites every field survey. All experiments were conducted from sunset to midnight at the Ogasawara Field Research Station of Tokyo Metropolitan University on Chichijima. Geckos were maintained at 25–29°C and 50–60% in relative humidity.

All analyses were conducted using R ver. 3.5.0 (R Development Core Team, 2018). To evaluate the effects of clones and sexes of the two gecko species on the contest rate, we built a generalized linear mixed effects model (GLMM) using the function GLMER in the lme4 package (Bates et al., 2015). In this case, we are not interested in which player won in each round, but are interested in which combination of players showed aggressive behavior. In GLMM (binomial errors with logit link), occurrence of contests (0 or 1) was treated as a response variable, and "combination of taxon groups" (taxon_pair), "distance form gecko to food" (D), "absolute difference in the SVL between players" (SVL), and "state of tails of both players" (T) were used as candidates of fixed effects. Because the same pairs were observed repeatedly (three times) in the experiment, pairs of individuals were incorporated into the model as a random effect in order to prevent the problem of pseudoreplication (Hurlbert, 1984). Eleven models with different combinations of fixed effects were evaluated; only taxon_pair, only D, only SVL, only T, taxon_pair+D, taxon_pair+SVL, taxon_pair+T, taxon_pair +D+SVL, taxon_pair+D+T, taxon_pair +SVL+T, and taxon_pair+D+SVL+T. Then, model selection was made based on Akaike Information Criterion (AIC), and the model with the minimum AIC was chosen as the best model (Burnham and Anderson, 2002). Regression coefficients in the best model were tested for statistical significance using Wald test with an alpha level of 0.05.

We also built GLMM (binomial errors with logit link) to test whether the four candidates of fixed effects, "taxon of individuals" (taxon), D, SVL, and T, are significantly related to the response variable, win/lose (1 or 0). "Taxon" was determined for both winner and loser in each round. Because the same pairs were observed repeatedly, pairs of individuals were incorporated into the model as the random effect. Eleven models with different combinations of fixed effects were evaluated; only taxon, only D, only SVL, only T, taxon+D, taxon+SVL, taxon+T, taxon+D+SVL, taxo +D+T, taxon+SVL+T, and taxon+D+SVL +T. Then, model selection was made based on AIC. Because the best model included only taxon (see Results), we used this model (explanatory variables=taxon, response variables=win or lose, error distribution=binomial distribution, link function=logit) to quantify and compare the strength in conflict between them using the 'Bradley Terry 2' package (Firth, 2005). The Bradley-Terry model (Bradley and Terry, 1952) assumes that in a "contest" between any two "players", say player i and player j ($i, j \in \{1, ..., K\}$), the odds that i beats j are $\alpha i/\alpha j$, where αi and αj are positive-valued parameters which might be thought as representing "fighting ability" (frequency of successful feeding in this study). Three rounds were counted as one game, and players that consume a large number of mealworms were defined as winners because Bradley-Terry model does not allow replicated data. The strength of Clone A was set to the reference value 0. The Bradley-Terry model was tested for statistical significance using Wald test, with an alpha level of 0.05.

RESULTS

The mean SVL was 39.8 mm (n=111, SD=1.5) in Clone A, 39.7 mm (n=102, SD=1.8) in Clone C, 53.5 mm (n=67, SD=0.9) in H-M, and 54.0 mm (n=68, SD=1.4) in H-F. The proportion of individuals with intact tails was 45 of 111 Clone A (40.5%), 96 of 102 Clone C (94.1%), 35 of 67 H-M (52.2%), and 40 of 68 H-F (58.8%). Thus, most individuals of Clone C had an intact tail in the field, and the proportion of individuals with intact tails was significantly different among the four groups ($\chi^2=69.4$, df=3, P<0.0001).

A total of 522 rounds by 174 pairs were observed. Contests occurred frequently in the combinations among individuals of Clone A, H-M, and H-F, whereas infrequently in those including Clone C (Table 1). Although body size of *L. lugubris* was smaller than *H. frenatus*, the frequency that Clone A engaged in contest was similar to that of *H. frenatus*.

In the contest rate, the best model included only "taxon_pair" based on AIC, and "D",

TABLE 1. Contests for food between two individuals of Clones A and C of *Lepidodactylus lugubris* and male and female *Hemidactylus frenatus*. The upper diagonal is filled by the number of observations (n) and frequency of contests (%), and the lower diagonal by the number of victories of each category. H-M: male *H. frenatus*, H-F, female *H. frenatus*.

Pairs	Clone A	Clone C	H-M	H-F
Clone A	n=54 83.3%	n=90 17.8%	n=72 66.7%	n=63 87.3%
Clone C	Clone A, 66 Clone C, 24	n=54 9.3%	n=42 7.1%	n=66 10.6%
H-M	Clone A, 34 H-M, 38	Clone C. 9 H-M, 33	n=27 100%	n=33 75.8%
H-F	Clone A, 33 H-F, 30	Clone C, 6 H-F, 60	H-M, 20 H-F, 13	n=21 90.5%

TABLE 2. The parameter estimates of regression coefficients of fixed effects in the best model of GLMM explaining the contest rates.

Parameter	Contest pair	Estimate	SE	z value	P value	
Intercept		1.067	0.362	2.951	0.0032	**
Taxon_pair	Clone A vs. Clone C	–1.247	0.422	–2.952	0.0032	**
	Clone A vs. H-F	–0.843	0.442	–1.906	0.0566	
	Clone A vs. H-M	0.063	0.399	0.157	0.8750	
	Clone C vs. Clone C	–2.431	0.474	–5.136	0.0001	***
	Clone C vs. H-F	–3.693	1.077	–3.429	0.0006	***
	Clone C vs. H-M	–2.215	0.518	–4.277	0.0001	***
	H-F vs. H-F	–0.971	0.570	–1.704	0.0884	
	H-F vs. H-M	–0.078	0.446	–0.174	0.8617	
	H-M vs. H-M	–0.536	0.636	–0.842	0.3996	

***P <0.001, **P<0.01

"SVL" and "T" were not recognized as important factors. Among regression coefficients of "taxon_pair" in the best model, in which the contest pair of Clone A vs. Clone A was used as standard, significantly negative values were obtained in four combinations of the contest pair that include Clone C (Table 2). No significant values were detected in regression coefficients of other contest pairs.

Clone C showed few aggressive behaviors such as arches, growls, bites, and lunges, and never exhibited wrestling, even in the interaction with the same clone (Fig. 2). Growls were the most frequent response in aggressive interactions among the combinations of Clone A, H-M, and H-F (Fig. 2). In four cases of combinations of Clone A and H-M, the tail was lost in three individuals of Clone A and one individual of H-M by biting of the opponent.

In examination of the factors affecting win/lose rate, the best model based on AIC included only "taxon", and "D", "SVL", and "T" were not recognized as important factors. Therefore, we used the Bradley-Terry model

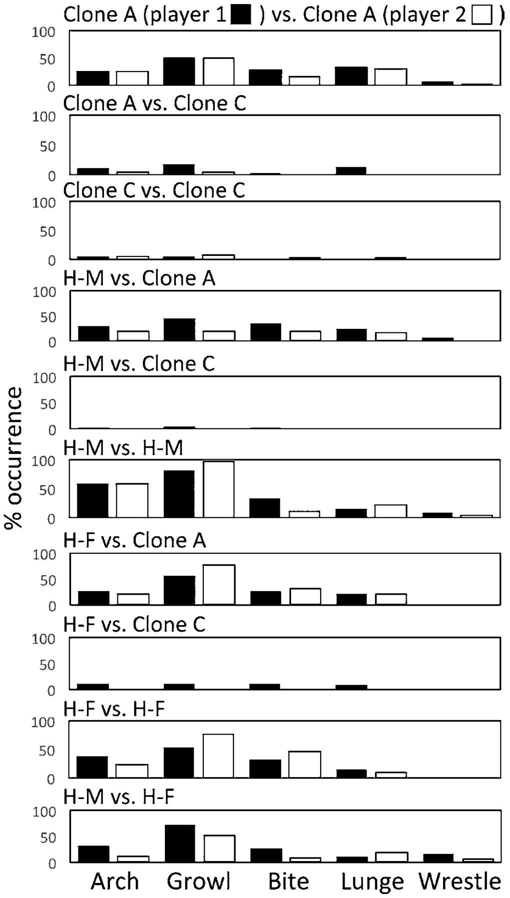

FIG. 2. Aggressive behaviors of players 1 and 2 when they interacted for a given prey item between two individuals of combinations of Clones A and C of *Lepidodactylus lugubris* and male and female *Hemidactylus frenatus* (H-M and H-F, respectively). Aggressive behaviors are shown in % occurrence of arches, growls, bites, lunges, and wrestles in the total number of rounds of two individuals.

only including taxon to quantify the fighting ability as win rate. The result suggested a superiority/inferior relationship among two clones of *L. lugubris* and *H. frenatus* (H-M>Clone A>H-F>Clone C). Clone C was found to have significantly lower fighting ability than Clone A (P<0.01; Fig. 3), but no significant differences were detected between Clone A and *H. frenatus*.

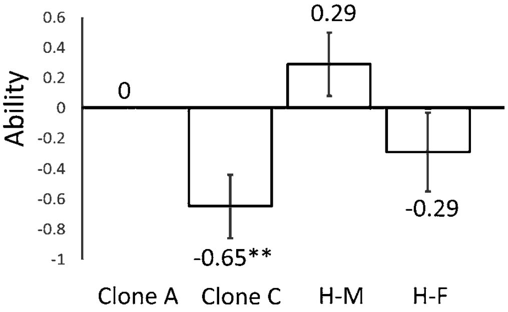

FIG. 3. Quantification of the fighting ability between two individuals of combinations of Clones A and C of *Leptodactylus lugubris* and male and female *Hemidactylus frenatus* (H-M and H-F, respectively), using the Bradley-Terry model. The strength of Clone A was set to the reference value 0. Bars indicate ±1SE. ** P<0.01.

DISCUSSION

In behavioral contests for food between two individuals in the small enclosure, Clone C of *L. lugubris* had a lower contest rate (frequency of feedings with some aggressive behaviors between individuals) and a lower fighting ability (frequency of successful feeding) than conspecific Clone A and both sexes of *H. frenatus*. Competition for food resources between geckos is affected by two factors: exclusive tendency (aggressive behavior towards other individuals) and foraging ability (strike distance, speed, and proportion of successive strikes) (e.g., Petren and Case, 1996). However, in the present study, we cannot distinguish all these factors. We found no significant effects of the distance to the food, body size difference in SVL, and state of tails on the contest rate and fighting ability.

Growls were the most frequent response in aggressive interactions in our experiment. However, we did not discriminate growls and clicks although clicks have been reported as a nonaggressive behavior (Dame and Petren, 2006). Therefore, our results of aggressiveness represented as growls may be overestimated. In behavioral observations, it is possible that some behaviors were actually emitted in a courtship context. However, any behavioral repertoire used in courtship (Dame and Petren, 2006) was not observed by male *H. frenatus* toward conspecific female in our experiments.

The behavioral tendency that Clone C was more timid than Clone A in contest rate and fighting ability could help to understand the distribution patterns of these two clones in the Ogasawara Islands. Artificial habitats in urban areas consist of typically flat building walls with artificial lights that attract insects. Therefore, insects, the lizards' primary prey, are abundant in small wall areas where competition to obtain these insects is severe. In this case, more aggressive individuals can eat more insects, and therefore timid individuals would be excluded from such an artificial area via long-term strong competition for food. In the Ogasawara Islands, the distribution of Clone A is biased towards the artificial environments such as house walls, electric poles, and road guardrails, whereas individuals of Clone C were found in natural area such as forests, rock crevices, grasslands, and beaches (Murakami et al., 2015). Our results suggest that differences in behavioral interactions may be one of the important factors affecting habitat segregation between Clones A and C. For Clone C, another cosmopolitan sexually reproducing gecko *Hemiactylus frenatus* may have the same impact as conspecific Clone A. If Clone C co-exists with *H. frenatus*, the similar distribution shift would be expected as in the case of coexisting with Clone A. However, their field distribution data are unavailable at present.

On the other hand, Clone A of *L. lugubris* had the high contest rate and fighting ability similar to both sexes of *H. frenatus* in their interactions. Aggressiveness including physical contacts may result in injury. In our observations, autotomy of the tail occurred in three individuals of Clone A and one male of *H. frenatus* by biting. In the field, most individuals of Clone C had intact tails, whereas a half of Clone A and *H. frenatus* had lost a part of their tails. This phenomenon may be explained by their different contest rates and aggressiveness.

Several researchers have reported behavioral interactions of *H. frenatus* and clones of *L. lugubris*. In Hawaii and Fiji, the proportion of *H. frenatus* relative to *L. lugubris* increases gradually in man-made arid environments, but the latter is relatively more common in more mesic and cooler environments (Case et al., 1994). Moreover, *H. frenatus* is more aggressive than Clones A and B of *L. lugubris* (Bolger and Case, 1992). If light is present, to which insects are attracted, *H. frenatus* dominates over *L. lugubris* by their aggressive interactions (Petren et al., 1993). Males of *H. frenatus* are more aggressive towards conspecific males, but show little aggression towards conspecific females and parthenogenetic *H. garnotii* (Dame and Petren, 2006). Females of *H. frenatus* and *H. garnotii* display little aggression (Dame and Petren, 2006). Our results also indicated males of *H. frenatus* are more aggressive than females although this is not statistically significant. Thus, *H. frenatus* (particularly males) is superior in interactions with parthenogenetic *L. lugubris* and *H. garnotii*. However, increases in both the dispersion of food resources and microhabitat topography have been known to reduce interspecific competition for food between *H. frenatus* and *L. lugubris* (Petren and Case, 1998). Interactions between Clones A and B of *L. lugubris* were also affected by habitat complexity (Short and Petren, 2008).

In our study, the superiority/inferior relationship among two clones of *L. lugubris* and both sexes of *H. frenatus* was estimated as H-M>Clone A>H-F>Clone C. Clone C interacted with other individuals less frequently and showed few aggressive behaviors. Our study demonstrates that the relationship among male and female *H. frenatus* and clones of *L. lugubris* is complex. In the future, we should examine the effects of regional differences in habitat structure, prey availability, and specific/clonal combinations to unravel such complexity in behavioral interactions among these geckos.

ACKNOWLEDGMENTS

We thank Tamotsu Kusano for his suggestion in statistical tests and two anonymous reviewers for their constructive comments. Samples were collected from protected areas with permission of the Ministry of the Environment, Japan (nos. 1607212, 1708251). All procedures of rearing and experiments of geckos were made after approved by the Tokyo Metropolitan University Animal Ethics Committee (A28-26 in 2016, A29-22 in 2017). This study was partially supported by Research Fellowships of the Japan Society for the Promotion of Science for Young Scientists (JP16J05260).

LITERATURE CITED

AVISE, J. C. 2015. Evolutionary perspective on clonal reproduction in vertebrate animals. *Proceedings of the National Academy of Sciences of the United States of America* 112: 8867–8873.

BATES, D., MÄCHLER, M., ZURICH, M., BOLKER, B. M., AND WALKER, S. C. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67: 1–48.

BOLGER, D. T. AND CASE, T. J. 1992. Intra- and interspecific interference behaviour among sexual and asexual geckos. *Animal Behaviour* 44: 21–30.

BOLGER, D. T. AND CASE, T. J. 1994. Divergent ecology of sympatric clones of the asexual gecko, *Lepidodactylus lugubris*. *Oecologia* 100: 397–405.

BOSCH, R. A. AND PÁEZ, R. B. 2017. First record from Cuba of the introduced mourning gecko, *Lepidodactylus lugubris* (Duméril et Bibron, 1836). *BioInvasions Records* 6: 297–300.

BRADLEY, R. A. AND TERRY, M. E. 1952. Rank analysis of incomplete block designs 1: The method of paired comparisons. *Biometrika* 39: 324–345.

BROWN, S. G., OSBOURNE, L. K., AND PAVAO, M. A. 1991. Dominance behavior in asexual gecko, *Lepidodactylus lugubris*, and its possible relationship to calcium. *International Journal of Comparative Psychology* 4: 211–220.

BURNHAM, K. P. AND ANDERSON, D. R. 2002. *Model Selection and Multimodel Inference: A Practical Information-theoretic Approach*. Springer, New York.

CASE, T. J. AND GILPIN, M. E. 1974. Interference competition and niche theory. *Proceedings of the National Academy of Sciences, U.S.A.* 71: 3073–3077.

CASE, T. J., BOLGER, D. T., AND PETREN, K. 1994. Invasions and competitive displacement among house geckos in the tropical Pacific. *Ecology* 75: 464–477.

COLE, C. J. 1984. Unisexual lizards. *Scientific American* 250: 94–100.

DAME, E. A. AND PETREN, K. 2006. Behavioural mechanisms of invasion and displacement in Pacific island geckos (*Hemidactylus*). *Animal Behaviour* 71: 1165–1173.

FIRTH, D. 2005. Bradley-Terry models in R. *Journal of Statistical Software* 12: 1–12.

GRASSMAN, M., BURTON, D., AND CREWS, D. 1991. Variation in the aggressive behavior of the parthenogenetic lizard (*Cnemidophorus uniparens*, Teiidae). *International Journal of Comparative Psychology* 5: 19–35.

HANLEY, K. A., BOLGER, D. T., AND CASE, T. J. 1994. Comparative ecology of sexual and asexual gecko species (*Lepidodactylus*) in French Polynesia. *Evolutionary Ecololgy* 8: 438–454.

HURLBERT, S. H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 54: 187–211.

INEICH, I. 1988. Mise en évidence d'un complexe unisexué-bisexué chez le gecko *Lepidodactylus lugubris* (Sauria, Lacertilia) en Polynésie française. *Comptes Rendus de l'Académie des Sciences, Série III* 307: 271–277.

INEICH, I. 1999. Spatio-temporal analysis of the unisexual-bisexual *Lepidodactylus lugubris* complex (Reptilia, Gekkonidae). p. 199–228. *In*: H. Ota (ed.), *Tropical Island Herpetofauna: Origin, Current Diversity, and Conservation*. Elsevier Science, Amsterdam.

INEICH, I. AND OTA, H. 1992. Additional remarks on the unisexual-bisexual complex of the gecko, *Lepidodactylus lugubris*, in Takapoto Atoll, French Polynesia. *Bulletin of the College of Science, University of the Ryukyus* 53: 31–39.

KEARNEY, M., FUJITA, M. K., AND RIDENOUR, J.

2009. Lost sex in the reptiles: constraints and correlations. p. 447–474. *In*: I. Schön, K. Martens, and P. von Dijk (eds.), *Lost Sex: The Evolutionary Biology of Parthenogenesis*. Springer, New York.

Leuck, B. E. 1985. Comparative social behavior of bisexual and unisexual whiptail lizards (*Cnemidophorus*). *Journal of Herpetology* 19: 492–506.

Moritz, C., Case, T. J., Bolger, D. T., and Donnellan, S. 1993. Genetic diversity and the history of pacific island house geckos (*Hemidactylus* and *Lepidodactylus*). *Biological Journal of the Linnean Society* 48: 113–133.

Murakami, Y. 2017. Clonal composition and distribution pattern of *Lepidodactylus lugubris* in the Mukojima Group of the Ogasawara Islands. *Ogasawara Kenkyu Nenpou* 40: 53–58.

Murakami, Y., Sugawara, H., Takahashi, H., and Hayashi, F. 2015. Population genetic structure and distribution patterns of sexual and asexual gecko species in the Ogasawara Islands. *Ecological Research* 30: 471–478.

Petren, K., Bolger, D. T., and Case, T. J. 1993. Mechanisms in the competitive success of an invading sexual gecko over an asexual native. *Science* 259: 354–358.

Petren, K. and Case, T. J. 1996. An experimental demonstration of exploitation competition in an ongoing invasion. *Ecology* 77: 118–132.

Petren, K. and Case, T. J. 1998. Habitat structure determines competition intensity and invasion success in gecko lizards. *Proceedings of the National Academy of Sciences, U.S.A.* 95: 11739–11744.

Paulissen, M. A. 2001. Ecology and behavior of lizards of the parthenogenetic *Cnemidophorus laredoensis* complex and their gonochoristic relative *Cnemidophorus gularis*: Implications for coexistence. *Journal of Herpetology* 35: 282–292.

R Development Core Team. 2018. R: A Language and Environment for Statistical Computing. *R Foundation for Statistical Computing*, Vienna, Austria.

Radtkey, R. R., Donnellan, S. C., Fisher, R. N., Moritz, C., Hanley, K. A., and Case, T. J. 1995. When species collide: The origin and spread of an asexual species of gecko. *Proceedings of the Royal Society of London B* 259: 145–152.

Radtkey, R. R., Becker, B., Miller, R. D., Riblet, R., and Case, T. J. 1996. Variation and evolution of Class I Mhc in sexual and parthenogenetic geckos. *Proceedings of the Royal Society of London B* 263: 1023–1032.

Schön, I., Martens, K., and Dijik, P. 2009. *Lost Sex: The Evolutionary Biology of Parthenogenesis*. Springer, Dordrecht.

Señaris, C., Runjaic, F. J. M. R., Aristeguieta, M. M., and Señaris, G. G. 2017. Second record of the invasive gecko *Lepidodactylus lugubris* (Duméril & Bibron, 1836) (Squamata: Gekkonidae) from Venezuela. *Journal of Species Lists and Distribution* 13: 1–4.

Short, K. H. and Petren, K. 2008. Boldness underlies foraging success of invasive *Lepidodactylus lugubris* geckos in the human landscape. *Animal Behavour* 76: 429–437.

Vrijenhoek, R. C. 1984. Ecological differentiation among clones: The frozen niche variation model. p. 217–231. *In*: K. Wohrmann and V. Loeschcke (eds.), *Population Biology and Evolution*. Springer-Verlag, Berlin.

Vrijenhoek, R. C. 1989. Genetic and ecological constraints on the origins and establishment of unisexual vertebrates. p. 24–31. *In*: R. M. Dawley and J. P. Bogart (eds.), *Evolution and Ecology of Unisexual Vertebrates*. New York State Museum, Albany.

Vrijenhoek, R. C., Dawley, C. J., Cole, C. J., and Bogart, J. P. 1989. A list of known unisexual vertebrates. p. 19–23. *In*: R. M. Dawley and J. P. Bogart (eds.), *Evolution and Ecology of Unisexual Vertebrates*. New York State Museum, Albany.

Weterings, R. and Vetter, K. C. 2018. Invasive house geckos (*Hemidactylus* spp.): Their current, potential and future distribution. *Current Zoology* 64. (in press)

Yamashiro, S., Toda, M., and Ota, H. 2000. Clonal composition of the parthenogenetic gecko, *Lepidodactylus lugubris*, at the northernmost extremity of its range. *Zoological Science* 17: 1013–1020.

Accepted: 7 July 2018