JOURNAL OF APPLIED ANIMAL WELFARE SCIENCE, *10*(3), 193–206

ARTICLES

Behavior as a Tool for Welfare Improvement and Conservation Management in the Endangered Lizard (*Gallotia bravoana*)

Gara Mesa-Avila and Miguel Molina-Borja
Lab. Etologia, Dept. Biologia Animal, Fac. Biologia
Universidad La Laguna, Canary Islands, Spain

The study assessed the behavior of *Gallotia bravoana* (La Gomera, Canary Islands, one of the world's most threatened reptiles) to facilitate management decisions and improve welfare during initial stages of a species' recovery plan. The study analyzed—and remote-controlled video cameras filmed—the behavior of lizards housed in 3 outdoor enclosures, from May to September 2000. Daily activity showed a bimodal or unimodal pattern, all specimens basking more during June, with the largest male was the most active. Adults ate a higher percentage of vegetable items; subadults, a comparatively larger proportion of larvae and adult insects. The study analyzed individual compatibility; all interacted during 2 short periods. Aggression occurred mainly between males; because most directed high-intensity aggression toward a specific lizard, the study recommended isolating this lizard in a separate enclosure. The study recommended keeping 2 male–female pairs, who demonstrated social tolerance, as breeding pairs in separated terraria. Typical courtship behavior (head-bob sequences) occurred mainly during July, with highest frequency by the oldest male. Behavioral assessment provided data for improving the individuals' welfare in the enclosures and to select specific pairs for breeding.

Correspondence should be sent to Miguel Molina-Borja, Lab. Etología, UDI Fisiología Animal, Facultad de Biología, Universidad La Laguna, 38206 La Laguna, Tenerife, Canary Islands, Spain. Email: mmolina@ull.es

Behavioral evaluation is widely recognized as a useful tool in conservation programs for threatened populations and/or species (Caro, 1998; Caro & Durant, 1995; Curio, 1996; Festa-Bianchet & Apollonio, 2003; Gosling & Sutherland, 2000; Sutherland, 1998). Ethological concepts, methods, and techniques have been used for different species and in different aspects of population recovery. For example, allowing females to choose between several potential mates has proved to be a successful way to increase the chances of producing offspring in some species (Burley, 1981; Partridge, 1980; Welch, Semlitsch, & Gerhardt, 1998). In addition, the use of model fathers increases the probability of chicks being imprinted on specific signals when raised in captivity (Immelmann, 1975; Lorenz, 1952; Toone & Wallace, 1994). Behavioral training of individuals against predators, when endangered species have to be bred and raised in captivity, is still another way to contribute to species recovery. Several studies have shown that this sort of training increases survival probability of the nonhuman animals once reintroduced into the wild (Griffin, Blumstein, & Evans, 2000; Griffin, Evans, & Blumstein, 2001; Mirza & Chivers, 2000; Wallace, 2000).

Unfortunately, most of the progress in the application of ethological principles and techniques in conservation has been done using mammals, birds, and some fish species; however, much less has been carried out with reptiles (Burghardt & Milostan, 1995). A population of *Lacerta agilis* was translocated as a way to contribute to its recovery following a fire in its natural area (Spellerberg & House, 1982). Eliminating potential egg predators as the kiore (*Rattus exulans*) from some New Zealand islets increased the recovery of some populations of the tuatara (*Sphenodon punctatus;* Cree, Daugherty, & Hay, 1991). Finally, the effect of anthropogenic habitat use on some lizard populations has also been analyzed (Díaz, Carbonell, Virgós, Santos, & Tellería, 2000; Lacy & Martins, 2003).

Underlying the application of all these conservation tools is a detailed knowledge of the behavior of the species under study—and of their predators or prey. In the present work, we report the results of a behavioral study conducted with six adult specimens of the greatly endangered lizard from the island of La Gomera in the Canary Islands (*Gallotia bravoana*) during their first year in outdoor terraria. The study was aimed at documenting behavioral features that could help improve the welfare during the maintenance and reproduction in captivity of the individuals, as part of a recovery program for the species ("head start program").

METHOD

Animals and Facilities

Subjects for this study were 4 male and 2 female adults of unknown age of the lizard G. bravoana from La Gomera in the Canary Islands (Bischoff, 1998; Hutterer, 1985; Nogales, Rando, Valido, & Martín, 2001). Table 1 gives biometric data. Measurements were taken the month before our study began.

TABLE 1
Biometric Data of the Specimens of *Gallotia bravoana* Studied

	Barbolo (Male)	*Colicorta (Female)*	*Clotildo (Male)*	*Ramona (Female)*	*Iballo (Male)*	*Che (Male)*
SVL	190	155	135	112	150	186
BW	460	190	337	310	450	184

Note. SVL = snout to vent length (in mm); BW = body weight (in g).

The lizards were discovered in 1999 in Risco de La Merica, a high inland cliff located in the southwest of La Gomera island and were initially kept in three outdoor terraria at Antoncojo (Alajeró, south of the island). Because of the restricted natural population, it was considered by local authorities that not more than the six individuals should be captured; therefore, we were not able to analyze a larger number of lizards.

Local natural plants and some stones were included inside the terraria (4 × 3 m each) to simulate a natural habitat; cork crusts were also provided as temporary shelters. The animals were fed 3 days a week with a diverse diet including larvae (Zoophoba), adult insects (grasshoppers and crickets), pieces of fruits (banana and mango), and leaves and flowers of the local plants tedera (Psoralea bituminosa) and balo (Plocama pendula). Water was always available in small bowls.

The three terraria were interconnected with plastic tubes (wider than lizard body width) running across the common walls; these pathways could be left opened or closed. Initially, lizards were separated into male–female pairs, but the connections were opened to allow social interactions and to evaluate the compatibility between individuals during two periods (June 21–June 27, 2000, and July 14–August 13, 2000). The rest of the time the pathways between the terraria were closed. The behavior of all specimens was videotaped by remote-controlled cameras, one per terrarium. After a few days, lizards became habituated to the slow movement of the cameras, and behavior was expressed normally. Up to 6 hr per day of animal activity were videotaped between the end of May and September 2000 (14 weeks, amounting to approximately 510 hr of recording).

From the data recorded, we initially compiled an ethogram; afterward, behavior was quantified in two different ways:

1. As relative frequency (by minute) and percentage of time of each behavior pattern for each individual; and
2. As frequencies of aggressive interactions (pooling throat inflation, biting attempts, and chasing pattern frequencies) between every pair of individuals (sociometric matrix).

Based on the matrix, we calculated an index of aggressive intensity among individuals as the difference between observed and expected frequencies of aggressive patterns between them. The expected frequencies were calculated from the matrix of observed ones, as: expected, frequency = (row total × column total)/grand total (de Vries, Nett, & Hanegraaf, 1993; Lehner, 1996), and the higher values of aggressive intensity (those with higher observed – expected frequencies) were represented in a flux diagram (Sustare, 1978).

In addition, food consumed was quantified as the percentage of different food items consumed—feeding episodes—by each animal during the recordings, and male courtship behavior was quantified as the number of head-bobbing sequences per day performed by each male during the breeding period. We also counted the duration of available, complete courtship sequences and the number of head bobs per second. Molina-Borja (1981, 1987, 1994) has described head-bobbing patterns in other *Gallotia* species.

Based on the data collected during the daily behavioral observations, specific recommendations were given to the staff in charge of the terraria to help in managing decisions of animal welfare. After our study concluded, the animals continued to be used as progenitors for the recovery program of the species in new outdoor terraria.

Statistics

Observed distributions of food types consumed and aggression frequencies between individuals were compared (program Mat Man; de Vries et al., 1993; Noldus, 2003), with the corresponding, expected distributions by means of the chi-square test (program Mat-Man 1.1; de Vries et al., 1993; Noldus, 2003) and the significance level set at $p < .05$. For the application of the chi-square test to a transition matrix, see Lemon and Chatfield (1971). We used the SPSS 12.0 for other statistical calculations.

RESULTS

Lizard activity followed a seasonal pattern, decreasing during the hottest months of the summer. For example, basking took a higher percentage of time during the end of May and June and decreased afterward in all animals (Figures 1a and 1b). Daily activity commonly began in the midmorning hours and ended after 17:30, following a bimodal pattern (Figures 2a and 2b).

Basking mainly occurred midmorning and late afternoon (Figure 1a). Lizards basked preferentially (data not shown) on two stones placed at different sides of the terraria.

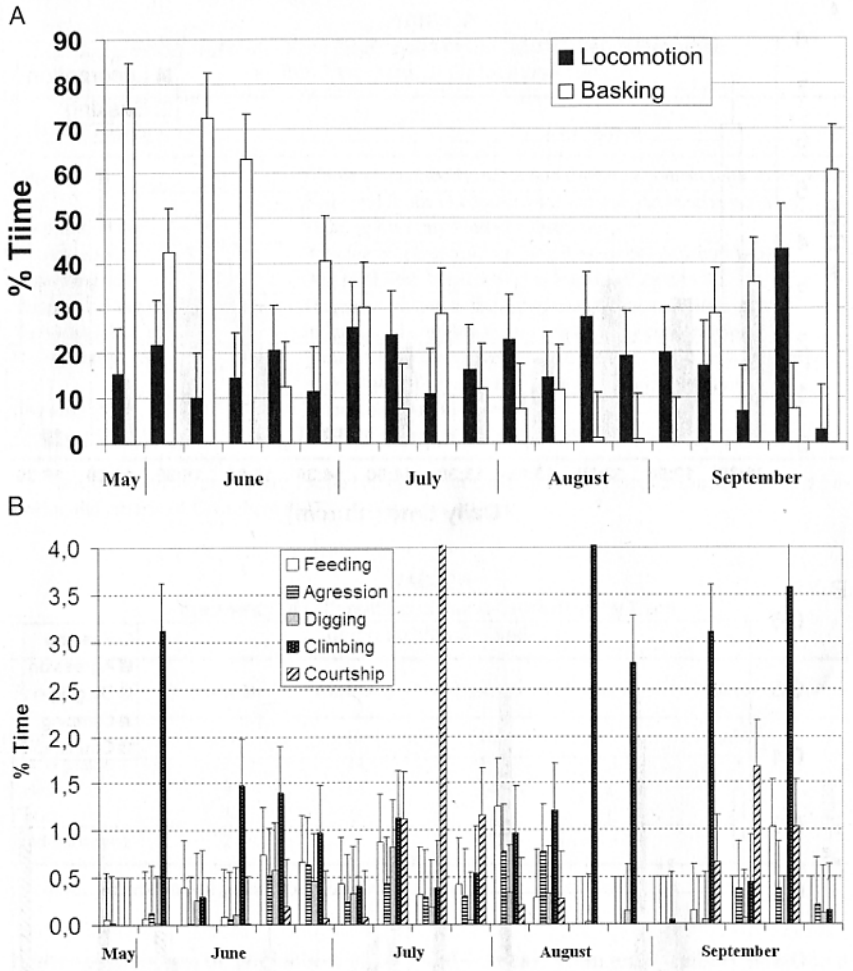

FIGURE 1 Mean (± SE) percentage of time (per week) dedicated to locomotion and basking (a) and other different behavior activities (b) by the lizards throughout the whole recording period, beginning the last week in May.

We constructed an ethogram that included those behavior patterns detected during our observations (Table 2). Most of the patterns are shared by other *Gallotia* species, but male head bobbing followed a species-specific pattern.

All specimens consumed a variety of the food types provided, but the percentage of items consumed by each lizard differed. Older (larger) animals consumed a

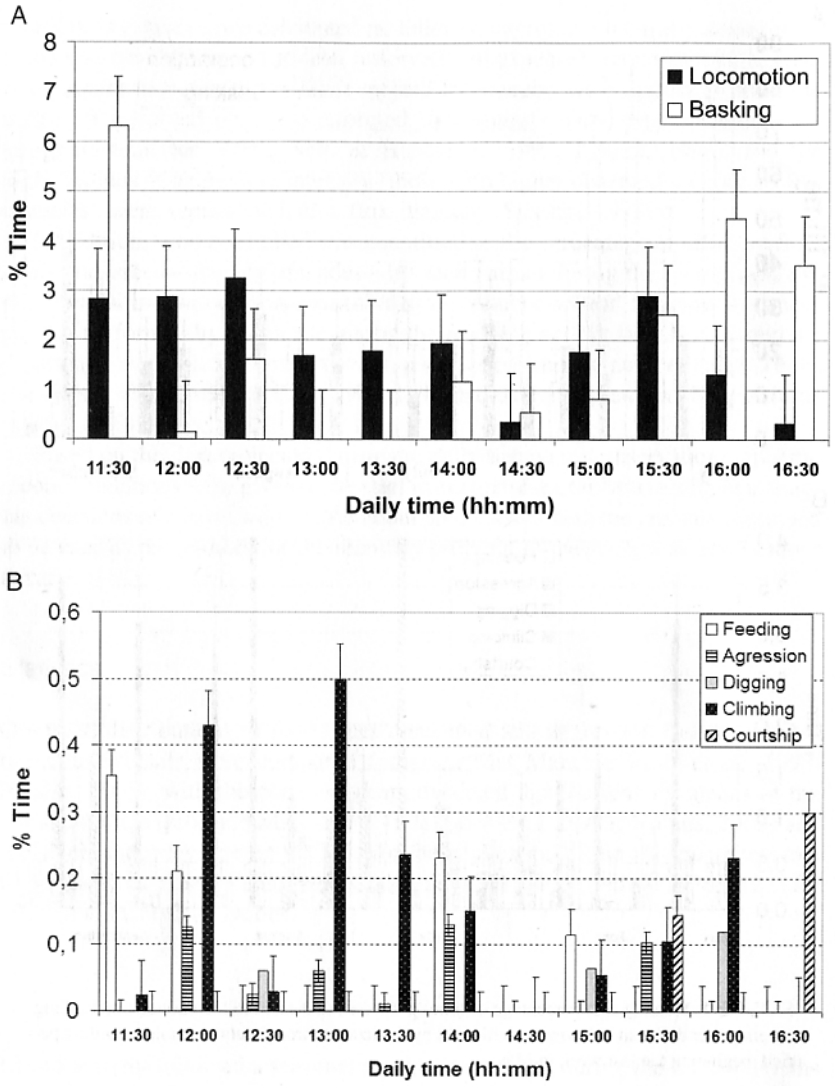

FIGURE 2 Mean (± SE) percentage of time that the animals dedicated to performing locomotion and basking (a) and other different behavior patterns (b) from midmorning to midafternoon hours.

TABLE 2
Name, Type and Brief Description of Behavior Patterns Recorded for the Specimens of *Gallotia bravoana*

Behavior Patterns	*Description*
Basking (S)	Whole animal (body, head, and limbs) in contact with substratum
Rest (S)	Body and limbs in contact with ground, but head is elevated
Locomotion (S)	Walking over any kind of substratum
Climbing (S)	Walking on plant trunk or branches, or on terrarium walls
Scratching (E)	One hind limb is quickly projected onto the head
Tongue flicking (E)	Tongue extrusion to the air or toward a conspecific
Throat inflation (S)	Inflating gular region together with body compression
Head bobbing (S)	Sequential up and down head movements while inflating gorge, usually performed while male walks around female
Chewing (S)	Processing food in the mouth
Digging (S)	Displace ground with forelimb claws

Note. Based on the previously detailed ethogram for *Gallotia galloti* (Molina-Borja, 1981) and following the criteria of Greenberg (1977). S = state; E = event.

TABLE 3
Frequency of Different Food Items Consumed by Each of the Lizards Studied

Food Type	*Barbolo*	*Colicorta*	*Clotildo*	*Ramona*	*Iballo*	*Che*
Fruits	20	10	10	1	10	2
Local plants	6	24	10	3	1	0
Insects	9	14	14	6	4	0
Feces	1	0	2	0	0	0
Undetermined	2	8	7	3	2	1

Note. Undetermined = nonrecognizable food items.

higher percentage of vegetables (fruits and leaves); younger (smaller) ones ate a higher percentage of insects (crickets, grasshoppers, and Tenebrio larvae). The difference between observed and expected values (Table 3) was significant, $\chi^2(20, N = 6) = 39.6$, $p < .01$.

When all lizards were allowed to interact by opening the connections between the terraria, the relative frequency of tongue flicking (considered to be a way to sample external chemical stimuli) increased for 2 males. On the other hand, aggression levels were higher between male individuals, although some females also interacted aggressively with other lizards. The higher aggression levels occurred from the oldest adult male toward the other males in the two interaction periods, $\chi^2(16, N = 5) = 225$, $p < .001$, and $\chi^2(16, N = 5) = 89.3$, $p < .001$, respectively, for each of the observed versus expected interaction-matrix comparisons (Figure 3).

Data from the male, Che, are not included because he was kept in an isolated terrarium. Iballo, the second-largest male in the group, received an unexpectedly high level of aggressive behavior patterns from other individuals. This information, gathered during social interactions, was used to recommend that the staff isolate this lizard in order to avoid undesirable aggression toward him.

Moreover, from the data obtained during the recording period, the behavioral compatibility between specific male–female pairs could be ascertained. For example, the largest adult male (Barbolo) and one of the adult females (Colicorta) while living together in a single terrarium did not show any potentially dangerous aggressive behavior and tolerated each other. Another pair of younger individuals also showed mutual tolerance. Based on these observations, it was recommended that these pairs be kept in an isolated terrarium for breeding purposes. This was achieved during the rest of the season and led to the establishment of the pairs who later showed courting and—in one of them—mating behaviors.

Typical courtship behavior consisted of a series of head-bobbing sequences. While moving around the female, the male inflated the gorge and performed vertical up and down head movements. This courtship was exhibited by the 2 males and occurred between the end of June and mid-September (Figure 4). The most intense courtship behavior was exhibited by the largest male, who performed up to 15 to 20 head-bobbing sequences in a single day during the month of July. The day with the highest courtship frequency by that male coincided with the single mating recorded (Figure 4). Mean time of courtship sequences was 24.5 ± 2.94 sec (complete sequences, $n = 56$) and 15.7 ± 1.7 sec (complete sequences, $n = 23$) for the larger and smaller male, respectively. Mean number of head bobs per second was 0.94 ± 0.28 and 1.00 ± 0.07 for the larger and smaller male, respectively.

DISCUSSION

Use of observations of individual lizard behavior (as a diagnostic tool) in conservation programs has not been very common in previous studies. However, there is evidence that behavioral traits can be critical in developing husbandry procedures for captive reptiles and determining how animals should be managed in the wild (Martins, 2004). For example, environmental enrichment has been used as a method to improve welfare in captive conditions in some reptiles such as turtles (Burghardt, Ward, & Rosscoe, 1996). Studies with other taxa have stressed the importance of adequate captivity conditions for the welfare of the studied individuals (Dawkins, 2003; Rabin, 2003). Our continuous behavioral assessment of individual lizards proved to be a very useful tool to help in their welfare during maintenance inside and in outdoor enclosures during the first breeding season in captivity. Taking into account that only 6 individuals of *G. bravoana* were available for the initial breeding program, we considered it very

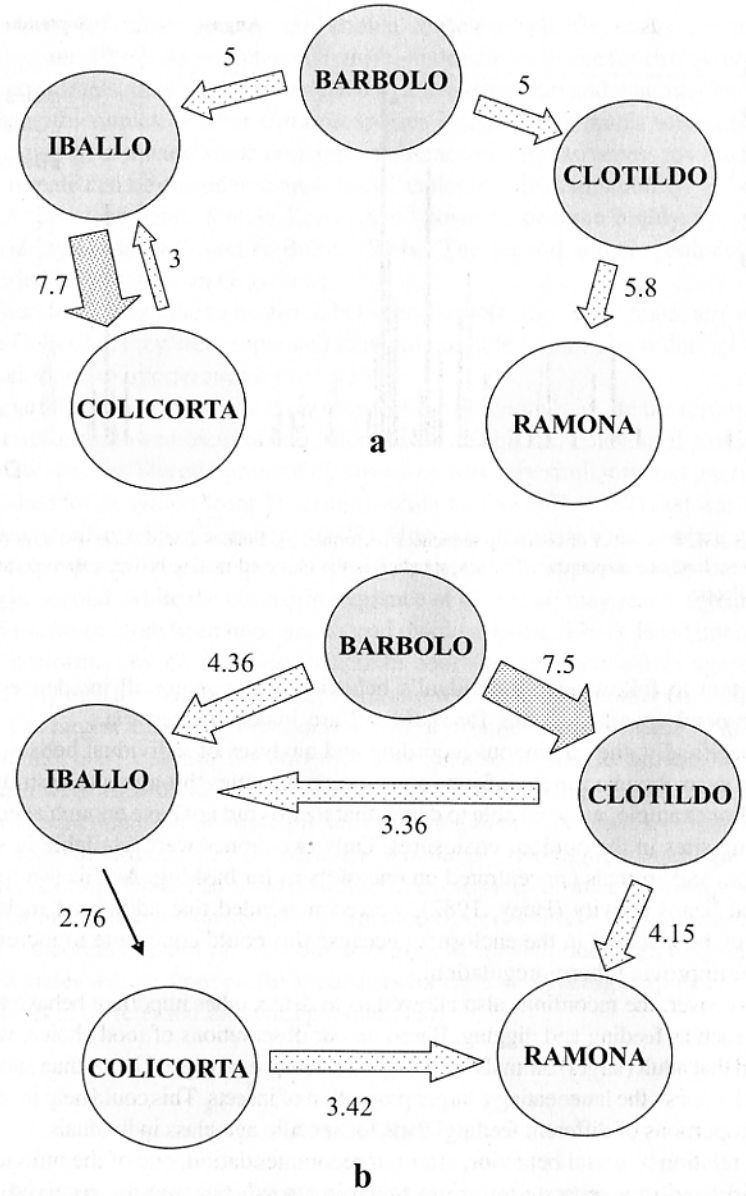

FIGURE 3 Aggressive interactions between all specimens June 21–June 27, 2000 (a) and July 14–August 13, 2000 (b). Arrow thickness is proportional to the observed minus the expected frequency (numbers close to arrows) of aggression between each pair of individuals. Darker circles correspond to males and lighter ones to females.

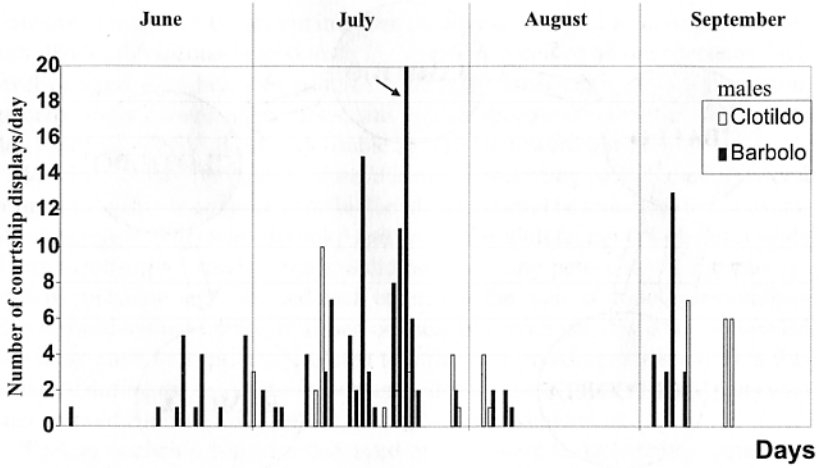

FIGURE 4 Number of courtship sequences performed by 2 males along successive days between June and September. The arrow indicates the observed mating between Barbolo and Colicorta.

important to follow each individual's behavior to document all incidences and recommend specific actions for their welfare inside the terraria.

Specifically, the continuous recording and analyses of individual behavior allowed us to obtain accurate information on their activities throughout the study period. For example, we were able to detect that lizards did not have enough adequate basking sites in the outdoor enclosures. Only two stones were available in some terraria, and animals concentrated on one of them for basking. As this is a fundamental lizard activity (Huey, 1982), we recommended that additional rocks for basking be installed in the enclosures because this could contribute to increasing and/or improving thermoregulation.

Moreover, the recordings also allowed us to detect other important behavior patterns such as feeding and digging. Based on our observations of food choice, we reported that adult (larger) animals ate a larger percentage of vegetal items than subadult (smaller ones), the latter eating a larger proportion of insects. This could help in selecting proportions of different feeding items for specific age-class individuals.

In relation to social behavior, after our recommendation, one of the individuals was isolated in a separate terrarium to avoid stressful aggression received from some other specimens when they were all allowed to interact. Dominance hierarchies usually develop even inside enclosures (Alberts, 1994) and may cause stress and affect development of smaller individuals (Berry, 1974; Phillips, Alberts, & Pratt, 1993).

Females of many species are known to select specific males for mating (Andersson, 1994). As we detected female–male pair tolerance for two pairs of the studied animals, they were kept isolated to allow courtship and mating. Our experience with couples of other *Gallotia* species indicates that males sometimes are very aggressive toward some females, so absence of aggressiveness toward a specific female can be considered an index of male–female compatibility.

On the other hand, female lizards are known to become highly aggressive around laying dates (Sloan & Baird, 1999). (The second author, Molina-Borja, provided information on *G. galloti*).

Therefore, after mating occurred between Barbolo, the oldest male, and the female Colicorta, they were separated to avoid possible female stress during laying behavior due to interference by the male.

Apart from contributing to the welfare of the individuals inside the terraria, our observations allowed us to obtain information on specific behavioral patterns of this new species. The ethogram of *G. bravoana* was very similar to that previously published for *G. galloti* from Tenerife (Molina-Borja, 1981, 1987) that was based on the criteria used by Greenberg (1977). However, the male head-bobbing courtship sequence followed a species-specific pattern with approximately one head bob per second, while the courtship sequence of *G. galloti* may reach a frequency of up to two or more head bobs per second (Molina-Borja, 1994). Head bobs were only performed by *G. bravoana* males in courtship interactions; in aggressive ones, only throat inflation occurred, similar to what happens in other *Gallotia* species. The largest male of *G. bravoana* showed a stronger courtship activity than did the smaller male, courting not only the larger but also the smaller female (when all animals were allowed to interact). In many of these courtship sequences, females showed rejection behavior patterns such as trying to bite the male, a behavior pattern also described for *G. simonyi machadoi* (Rodríguez-Domínguez, & Molina-Borja, 1998). The analysis of the characteristics of male courtship behavior that are important for female acceptance deserves future attention, not only from a theoretical point of view but also from an applied one (e.g., to determine which males will be more useful as partners for captive breeding purposes or as individuals to be released into wild populations).

CONCLUSIONS

Our observations during this study enabled us to reach a number of conclusions as to the lizards' activity level, preferred diet, and behavior (from aggressive to courtship). We ascertained normal lizard daily activity that showed a bimodal or unimodal pattern, the largest male having a higher activity level than the other individuals. Specimens showed a normal basking pattern, dedicating more time

during June than in the following months. Following our behavioral observations, we recommended increasing basking sites (stones) in the terraria.

In addition, we ascertained differences in adult and subadult diets (higher percentage of vegetable items than other types of food and a comparatively larger proportion of larvae and adult insects, respectively) that could serve to establish more specific diets depending on age.

Our analysis of aggressive behaviors between individuals helped to detect compatibility between them and avoid possible stressful situations. Thus, after our recommendation, one individual was isolated in a separate enclosure because most other individuals had directed aggressive behavior toward him. However, members of two specific male–female pairs tolerated each other; after our recommendation, they were kept separated as breeding pairs, and one pair showed mating behavior. We observed that courtship behavior (sequences of head bobs) was performed normally by the oldest male and a younger male, mainly during July, with the former displaying the highest frequency of courtship behavior. Our behavioral assessment formed the basis of making alternations to improve the welfare of the animals in the enclosures and also to select specific pairs for breeding.

ACKNOWLEDGMENTS

The Consejería de Política Territorial y Medio Ambiente of the Canarian Government funded this work. We thank Cristina Suárez, Javier Hernández, and Ana Román for help in recording lizard activity during part of the study; Enrique Font for helpful comments on an earlier version of the article; Olav Hitten and Carmen D. Arzola, the staff at the terraria installations on La Gomera, for their continuous daily help in the maintenance of lizards and terraria; and Miguel A. Rodríguez-Domínguez for help in sexing the individuals. We are also thankful for collaboration from the staff of the Cabildo de La Gomera (local island government).

REFERENCES

Alberts, A. C. (1994). Dominance hierarchies in male lizards: Implications for zoo management programs. *Zoo Biology, 13,* 479–490.

Andersson, M. (1994). *Sexual selection*. Princeton, NJ: Princeton University Press.

Berry, K. H. (1974). The ecology and social behavior of the chuckwalla (*Sauromalus obesus obesus* Baird). *University of California Publications, Zoology, 101,* 1–60.

Bischoff, W. (1998). Bemerkungen zu den "fossilen" Rieseneidechsen der Kanarischen Inseln. [Remarks on the "fossil" giant lizards of the Canary Islands]. In W. Bischoff (Ed.), *Handbuch der Reptilien und Amphibien Europas: Bd. 6. Die Reptilien der Kanarischen Inseln, der Selvagens-Inseln und des Madeira Archipels* (pp. 387–407). Wiesbaden, Germany: Aula-Verlag.

Burghardt, G. M., & Milostan, M. (1995). Ethological studies on reptiles and amphibians: Lessons for species survival. In J. Demarest, B. Durrant, & E. Gibbons (Eds.), *Captive conservation of endangered species: An interdisciplinary approach* (pp. 187–203). New York: State University of New York Press.

Burghardt, G. M., Ward, B., & Rosscoe, R. (1996). Problem of reptile play: Environmental enrichment and play behaviour in a captive Nile soft-shelled turtle. *Zoo Biology, 15,* 223–228.

Burley, N. (1981). Sex ratio manipulation and selection for attractiveness. *Science, 211,* 721–722.

Caro, T. (Ed.). (1998). *Behavioural ecology and conservation biology*. New York: Oxford University Press.

Caro, T. M., & Durant, S. M. (1995). The importance of behavioural ecology for conservation biology: Examples from studies of Serengeti carnivores. In A. R. E. Sinclair & P. Arcese (Eds.), *Serengeti: Vol. 2. Dynamics, management and conservation of an ecosystem* (pp. 451–472). Chicago: University of Chicago Press.

Cree, A. C., Daugherty, H., & Hay, J. M. (1991). Reproduction and conservation of rare populations of tuatara (*Sphenodon punctatus*) on offshore islands of New Zealand. In *Proceedings of the 60th Congress of the Australian and New Zealand Association for the Advancement of Science: Section A. Reproduction in animals*. Adelaide, Australia: University of Adelaide.

Curio, E. (1996). Conservation needs ethology. *Trends in Ecology and Evolution, 11,* 260–263.

Dawkins, M. (2003). Behaviour as a tool in the assessment of animal welfare. *Zoology, 106,* 383–387.

de Vries, J., Nett, W. J., & Hanegraaf, P. L. H. (1993). Matman: A program for the analysis of sociometric matrices and behavioural transition matrices. *Behaviour, 125,* 157–175.

Díaz, J. A., Carbonell, R., Virgós, E., Santos, T., & Tellería, J. L. (2000). Effect of forest fragmentation on the distribution of the lizard (*Psammodromus algirus*). *Animal Conservation, 3,* 235–240.

Festa-Bianchet, M., & Apollonio, M. (2003). *Animal behavior and wildlife conservation*. Washington, DC: Island Press.

Gosling, L. M., & Sutherland, W. J. (Eds.). (2000). *Behaviour and conservation*. Cambridge, UK: Cambridge University Press.

Greenberg, N. (1977). An ethogram of the blue spiny lizard (*Sceloporus cyanogenys*) (Sauria, Iguanidae). *Journal of Herpetology, 11,* 177–195.

Griffin, A. S., Blumstein, D. T., & Evans, C. S. (2000). Training captive-bred or translocated animals to avoid predators. *Conservation Biology, 14,* 1317–1326.

Griffin, A. S., Evans, C. S., & Blumstein, D. T. (2001). Learning specificity in acquired predator recognition. *Animal Behaviour, 62,* 577–589.

Huey, R. B. (1982). Temperature, physiology, and the ecology of reptiles. In C. Gans & F. H. Pough (Eds.), *Biology of the reptilia* (Vol. 12, pp. 25–91). London: Academic.

Hutterer, R. (1985). Neue funde von Rieseneidechsen auf der Insel Gomera (*Lacertidae*) [New investigation on the giant lizard (*Lacertidae*)]. *Bonner zoologische Beiträge, 36,* 365–394.

Immelmann, K. (1975). Ecological significance of imprinting and early learning. *Annual Review of Ecology and Systematics, 6,* 15–37.

Lacy, K. E., & Martins, E. P. (2003). The effect of anthropogenic habitat usage on the social behaviour of a vulnerable species (*Cyclura nubile*). *Animal Conservation, 6,* 3–9.

Lehner, P. N. (1996). *Handbook of ethological methods*. New York: Cambridge University Press.

Lemon, R. E., & Chatfield, C. (1971). Organization of song in cardinals. *Animal Behaviour, 19,* 1–17.

Lorenz, K. Z. (1952). *King Solomon's ring*. New York: Crowell.

Martins, E. (2004). Introduction. In A. C. Alberts, R. L. Carter, W. K. Hayes, & E. P. Martins (Eds.), *Iguanas: Biology and conservation* (pp. 97–100). Berkeley: University of California Press.

Mirza, R. S., & Chivers, D. P. (2000). Predator-recognition training enhances survival of brook trout: Evidence from laboratory and field-enclosure studies. *Canadian Journal of Zoology, 78,* 2198–2208.

Molina-Borja, M. (1981). Etograma del lagarto de Tenerife (*Gallotia galloti galloti*) (Sauria-Lacertidae) [Ethogram of the Tenerife lizard (*Gallotia galloti galloti*) (Sauria-Lacertidae)]. *Doñana Acta Vertebrata, 8,* 43–78.

Molina-Borja, M. (1987). Additions to the ethogram of the lizard (*Gallotia galloti*) from Tenerife, Canary Islands. *Vieraea, 17,* 171–178.

Molina-Borja, M. (1994). First graphical representation (display-action-pattern graph) of male headbobbing display in a lacertid (*Gallotia galloti eisentrauti*). *Etología, 4,* 93–97.

Nogales, M., Rando, J. C., Valido, A., & Martín, A. (2001). Discovery of a living giant lizard, genus *Gallotia* (*Reptilia: Lacertidae*), from La Gomera, Canary Islands. *Herpetologica, 57,* 169–179.

Noldus Information Technology. (2003). *MatMan reference manual* (Version 1.1). Wageningen, The Netherlands: Author.

Partridge, L. (1980). Mate choice increases a component of offspring fitness in fruit flies. *Nature, 283,* 290–291.

Phillips, J. A., Alberts, A. C., & Pratt, N. C. (1993). Differential resource use, growth and the ontogeny of social relationships in the green iguana. *Physiology & Behavior, 53,* 81–88.

Rabin, L. A. (2003). Maintaining behavioural diversity in captivity for conservation: Natural behaviour management. *Animal Welfare, 12,* 85–94.

Rodríguez-Domínguez, M. A., & Molina-Borja, M. (1998). Reproduction of the endangered Hierro giant lizard (*Gallotia simonyi machadoi*). *Journal of Herpetology, 32,* 498–504.

Sloan, C., & Baird, T. (1999). Is heightened post-ovipositional aggression in female collared lizards (*Crotaphytus collaris*) nest defense? *Herpetologica, 55,* 516–522.

Spellerberg, I. F., & House, S. M. (1982). Relocation of the lizard *Lacerta agilis:* An exercise in conservation. *British Journal of Herpetology, 6,* 245–248.

Sustare, D. (1978). Systems diagrams. In P. W. Colgan (Ed.), *Quantitative ethology* (pp. 275–311). New York: Wiley.

Sutherland, W. J. (1998). The importance of behavioural studies in conservation biology. *Animal Behaviour, 56,* 801–809.

Toone, W. D., & Wallace, M. P. (1994). The extinction in the wild and reintroduction of the California condor (*Gymnogyps californianus*). In P. J. S. Olney, G. M. Mace, & A. T. C. Feistner (Eds.), *Creative conservation* (pp. 411–419). London: Chapman & Hall.

Wallace, M. P. (2000). Retaining natural behaviour in captivity for re-introduction programmes. In L. Morris Gosling & W. J. Sutherland (Eds.), *Behaviour and conservation* (pp. 300–314). Cambridge, UK: Cambridge University Press.

Welch, A. R., Semlitsch, D., & Gerhardt, H. C. (1998). Call duration as an indicator of genetic quality in male gray tree frogs. *Science, 280,* 1928–1930.