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How habitat disturbance benefits geckos: Conservation implications

Comment les perturbations de l'habitat bénéficient aux geckos – implications pour leur conservation

Ivan Ineich

CP 30 (reptiles), CNRS UMR 7205 (origine, structure et évolution de la biodiversité), Muséum national d'histoire naturelle, département de systématique et évolution, 25, rue Cuvier, 75005 Paris, France

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ABSTRACT

I here provide some field observations and literature data showing that egg laying site availability could be the main limiting factor for most arboreal gecko population dynamics. Several natural (typhoons, volcanism, sea level variations) or human-mediated habitat modifications (garden openings in forested areas) provide enough habitat disturbances to significantly increase reproductive outputs in island gecko populations. Such observations, however, also apply to continental populations. Our observations suggest that artificial shelter and egg laying site creation could easily allow populations to increase and also supply easier access to arboreal species for ecological or biodiversity studies. Furthermore, our observations also point out that occurrence in man-made habitats and genetic uniformity of most widespread island lizards should not be considered as evidence of their recent introduction through human agency.

RÉSUMÉ

Nous présentons ici quelques observations réalisées sur le terrain et des données provenant de la littérature montrant que la disponibilité des sites de ponte pourrait être le principal facteur limitant la dynamique des populations de geckos arboricoles. Les modifications naturelles des habitats (typhons et cyclones, volcanisme, variations des niveaux marins) ou celles engendrées par l'homme (ouverture de petits jardins dans de vastes zones couvertes de forêt) provoquent assez de perturbations pour augmenter significativement la reproduction des populations insulaires de geckos. De telles observations semblent également s'appliquer aux populations continentales. Nos résultats suggèrent que la création d'abris et de sites de ponte artificiels pourrait facilement permettre d'accroître certaines populations en déclin mais également fournir aux scientifiques un accès plus aisé aux geckos arboricoles et à leurs pontes dans le cadre d'études écologiques ou de biodiversité. De plus, notre étude montre également que l'anthropophilie et l'uniformité génétique de la majorité des lézards insulaires ne doivent pas être considérés comme des preuves de leur introduction récente par l'homme.

1. Introduction

Tropical island lizards mostly belong to two families which are also the most widespread and diverse lizard

E-mail address: ineich@mnhn.fr.

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families, globally skinks (Scincidae) and geckos (Gekkonidae). This is particularly true on tropical Pacific islands [1,2]. However, my unpublished field observations seem to show that their population dynamics related to man-made disturbances is completely different. Skink densities seems not really to vary according to areas perturbed or unperturbed by man. This situation is not the same for geckos as most of their widespread species show significant and higher densities in and around habitats disrupted by man. The purpose of this paper is to identify some explanations for my observation and to relate it on to perspectives on gecko conservation.

Food is certainly more abundant around the man-perturbed areas. Most of these geckos and skinks feed on arthropods, and yet those animals making up their diet do not seem to be limited on the majority of islands in either pristine or disturbed habitats. It should not be overlooked that artificial lights attract some night active geckos because they promote the aggregation of insect prey. Thus, other factors than food availability are probably responsible for the observed density differences between the two families in modified and pristine habitats. One of the most evident limiting factors is suitable egg laying sites. Skinks lay their eggs in soil (sometimes inside old dead trees fallen down) or ground debris [3–5]. Therefore, they are weakly dependent on man and habitat modifications as they can lay their eggs similarly in both kinds of habitats, natural or perturbed. This is even true for arboreal or semi-arboreal skink species, all depending on the ground level to lay their eggs, contrary to arboreal geckos. On the one hand, it can explain why skink densities are similar in both altered and unaltered habitats, except of course when habitat has been opened for a species requiring only closed conditions or when other important modifications have occurred. In addition, the impact of human-associated lizard predators like pigs or cats on skinks or terrestrial geckos can be important. On the other hand, most arboreal island geckos are dependent on favourable trees (dead or alive but with loose bark), banana trees in gardens, or other substrates (e.g., house decks made in *Pandanus* spp. leaves) to lay their eggs [4,6]. Thus, their situation is clearly different and man-made modifications significantly increase the number of suitable egg laying sites for geckos. The below-mentioned observations concern island ecosystems but they may also apply to most tropical continental ecosystems, including Amazonia.

2. Scarcity of laying sites for arboreal geckos

Unquestionably, densities of most of these forest arboreal geckos are relatively low in their natural habitat [7]. They are often more abundant in and around disturbed habitats as can be seen, e.g., for *Lepidodactylus lugubris*. That species is occasionally found in disturbed forests, rock outcrops, and gardens, but reaches its greatest densities on buildings [3]. Zug [3] also noted that *Gehyra oceanica* occurs both as a human commensal and in forests. Its occurrence on buildings often tends to be associated with rural conditions where forests and gardens are nearby, thus suggesting forests are its natural habitat. On tropical Pacific and Indian Ocean islands, such high densities of geckos in and around disturbed areas are usually interpreted as a demonstration of their recent arrival and dispersion through human-mediated transportation, even if those species can also be observed in pristine habitats but with very low densities [8–10].

In fact, I suggest that their low density could actually be the natural state and that increased density in and around man-made habitats is the result of the artificial development of egg laying sites availability. Finding gecko eggs is easy in man disturbed habitats in e.g. French Polynesia but is a difficult task in forest except on dead tree trunks. Under no circumstances can the lizard high densities around human-disturbed habitats prove their recent arrival on those islands. One recently described endemic Vanuatu gecko, *Lepidodactylus vanuatuensis*, which is sometimes common on trees in and around villages has not been recently introduced by man. Its occurrence in this habitat is simply related to its ecological requirement for open and relatively mesic habitats since it is not a forest species. I commonly find its eggs under the bark of introduced trees like mango or *Casuarina equisetifolia*, thus showing that native trees provide only limited favourable egg laying sites.

While walking in a natural undisturbed forest, I was surprised at the difficulty of finding dead trees, or even trees with loose bark allowing geckos to shelter and lay eggs between it and the tree cambium. If such a tree could be found, the richness of lizards and eggs on this sole tree was always spectacular. It is possible to walk one day in a closed forest on an island in French Polynesia without seeing one gecko but when finding a dead tree in the same forest you can easily see 20+ geckos (males, females and juveniles). Comparative quantitative data are not available for such observations but could easily been obtained. Furthermore, several distinct species could develop there in complete syntopy, sometimes including eggs of different species found together. Such an observation could easily be made in and around small village gardens, which were directly opened in the pristine forest (e.g., in Vanuatu), often separated from the village by several hundred meters or even kilometres (as is also true on continents). Lizard density in such artificially open habitats is clearly significantly increased compared to surrounding forest. Skink density is augmented there because most of these lizards need sun and open habitats allowing their thermoregulation. They constantly had to move on the forest ground to follow small mobile sun patches. Population estimates were made by Zug [1] on two Fiji islands. He found a density of 1390 *Emoia cyanura* ha^{-1} along a small stream in an overgrown pasture whereas that density increased threefold to 4090 ha^{-1} in a recently cleared taro garden on a gently slopping hillside. Besides, geckos found there numerous dead trees often killed by villagers but left until dried ultimately in order to be burned. The use period of such a dead tree for geckos was of several months, thus becoming a significant egg laying site once its bark was coming off the cambium, creating in the same way a space serving as a shelter for the animal and eggs. Small geckos like *L. lugubris* can lay clutches of 2 eggs at least 8 times a year (Ineich, unpubl. data). Such small opened ‘*islands within the island*’ (i.e., the gardens) often attracted true forest lizard species that could only rarely be observed in the forest. There is no doubt that gardens have been participating in the lizard population dynamic for a long time in a positive way coinciding with human settlings. Contrary to these small yards, large-scale gardens or plantation forests are dominated by wide-ranging habitat generalists [11]. Several years ago, I was in the field with Zug (Smithsonian Institution) to sample lizards on the Fiji islands. We found a place where many trees were killed but still standing. Their base was sawn circularly several millimetres deep to prevent root food from reaching the trunk. This operation had been made several months before our arrival. Dead standing trees offered a nice space between the bark and the cambium. When detaching the bark we found very high, almost exceptional, densities of an uncommon gecko species (*Lepidodactylus manni*), of which only few specimens were present in collections until then [12]. In this case, human action clearly boosted the population dynamic of this gecko, allowing high densities that were never found anywhere else. One would erroneously conclude that the species was abundant there because man introduced it accidentally, which does not make any sense here. That species was just an endemic forest gecko that discovered favourable and abundant egg laying sites in this man-made artificial place. In the present instance, egg laying sites and shelter availability were obviously the limiting factors explaining low density of that species elsewhere. Pacific island geckos like *Gehyra oceanica* or *L. lugubris*, very often considered as recent man-mediated colonists, did not really prefer forest nevertheless they still lived there. When a small garden shed was created surrounded by forest, both species could easily be found, even though it was far from the nearest village. Thus, both species should be naturally present in the forest, even if rarely seen in that kind of habitat, which could be experimentally tested in the future. In that artificial opening and the newly created shelter (e.g. the garden sheds), they were more easy to observe and can find egg laying sites and refuges so that their density increased. In such artificial '*island*' habitats inside large forest patches, the recently introduced gecko *Hemidactylus frenatus*, a classical alien species on tropical Pacific islands, was never found. If man had introduced both previous species into inland forest, he would also have introduced that alien and ecologically aggressive species. In continental forested areas, the situation seems to be similar. In French Guiana, when a camp is built far inside the forest, several gecko species, previously scarce, become common after several months, like *Gonatodes humeralis*. This could also be connected with the increased availability of egg laying sites and shelters inside and around the new camp. Specimens of *G. humeralis* can be seen on tree trunks around the new camp from where they were lacking previously and observations include juveniles. Quantitative data on such observations are lacking.

3. Replacement egg laying sites

We now have to answer a first question: if there are so few egg laying sites and shelters for geckos in forest, how do they lay their eggs? Communal egg laying is a very common feature of lizards [4,13,14], including many skinks [13,15,16] and geckos [13,17,18], particularly developed on islands. In fact, this characteristic has a double explanation. First, it partly explains the scarcity of available and favourable egg laying sites, so that when such a site is available it is used by several females. Second, it is also related to biogeographical characteristics of those animals which are clearly specialized and efficient island colonists. Communal egg laying (associated with adhesive eggs) has certainly been selected during their evolution by allowing them to colonize virgin islands by rafting through an initial population (as eggs and individuals or just as eggs) and not just one individual, like parthenogenesis allows, which is also common to those island specialized lizards. Dead trees, or at least favourable ones for geckos to lay their eggs, are scarce in pristine forests. Geckos have, however, found several replacement egg laying sites to survive. I have often seen gecko eggs laid in wasp nests (particularly pompilid wasps) in Vanuatu or in French Polynesia. In the same way, eggs of the rarely encountered endemic gecko *Urocotyledon inexpectata* have also been observed in wasp nests, in the Seychelles (S. Rocha, pers. comm.). Eggs are also often deposited on the particular leaves of *Pandanus* trees, which are common on the sea border (e.g. Tuamotu atolls) but not really in forests, or in dead trees and empty dead tree ferns when available. Rock cracks are commonly used by several gecko species like *Gehyra oceanica* or *L. lugubris*, particularly in limestone areas (fossil coral rocks). The softness of gecko eggshell when laid allows its shape to vary before hardening and reaching its normal shape once placed in the crack. During a recent field trip to Vanuatu, I saw numerous gecko eggs in epiphytic myrmecophytes hanging on tree trunks, sometimes more than 20 meters high. Such epiphytic plants, sometimes weighing more than 20 kg, had numerous small cavities, some occupied by ants and others devoid of ants, the latter one being used by geckos to lay their eggs. I there found many eggs of uncommon typical forest species like the giant *Gehyra vorax*, a species rarely observed in the wild, and a new species recently described (*Lepidodactylus buleli*; [7]), as well as their eggs. In the same way, the rare gecko *Hemiphyllodactylus typus* and its eggs were also observed in an epiphytic myrmecophyte (*Dischidia rafflesiana*) in Sarawak [19]. On La Réunion Island in the Mascarenes (Indian Ocean), it is common to find geckos and their eggs (*Phelsuma* sp., *Hemiphyllodactytlus typus*) in metallic road signs, far from human habitations along sunny roadsides [20].

4. Egg laying sites availability: vulcanism and typhoon impacts

A second question remains: are there historical events that lead to significant decrease or increase of gecko abundance? One factor causing a decrease to gecko density would be, of course, related to the forest's complete destruction without giving time to geckos to use dead trees. Vulcanism is certainly an agent of species extinction on some islands. It, however, could be an important factor of gecko population dynamic in the western tropical Pacific area, particularly in countries like Vanuatu or the Solomon Islands [1]. Huge forested areas can be completely burned. This should clearly have a negative impact on gecko densities and may have favoured speciation under some conditions, perhaps by separating populations with a subsequent low reproductive rate due to poor egg laying site availability, or inversely having a positive impact on gecko densities by creating numerous egg laying sites inside dead burned tree trunks. The second common event in the area is typhoons. They likely constitute the most frequent mover to 'regularly' (at a historical scale) boost gecko population dynamic. They do not destroy the forest but create a huge amount of suitable egg laying sites for geckos. Their frequency is elevated. Cocos Atoll in the Mariana Islands has undergone at least three severe magnitude typhoons since 1949 that have devastated the island [21]. They are a yearly event on most tropical Pacific and Indian Ocean islands.

Few biological studies on typhoon effects on ecosystems are available for Pacific islands [22], most of them concerning hurricanes in the Caribbean islands [23–25]. Damage on trees following a hurricane is estimated in the Caribbean. Few trees died and mortality was assessed between 1–13% according to the locality. Clear adaptations of trees to hurricanes have emerged from the available studies [26–28]. Tall trees and trees with large diameters were most likely to be uprooted [29]. Hurricane impact on animals is poorly understood but all studies agree that they should be considered as an important factor for animal evolution in areas subject to their impact. They can greatly affect some animal populations, including freshwater fishes, for which storm-induced drift dispersal has been observed [30], or atyid shrimps for which abundance has increased through an unusual food resource availability (decomposing leaves and algae) following a hurricane [31]. Amphibians have shown a rise in density after Hurricane Hugo (1989) for some species at least (fourfold), explained by an increase in retreat sites and a decrease in invertebrate predators [32]. A 25-year study has demonstrated that colour pattern differences were clearly associated to habitat. The comparison of colour-morph frequencies through time and in the same sites has shown temporal shifts by the frog *Eleutherodactylus coqui* immediately occurring after Hurricane Hugo in 1989. Authors suggest that the pattern polymorphism is partially maintained thanks to local habitat matching resulting from visual predators-induced selection pressure. Thus, the hurricane has had a direct influence on population dynamic [33]. However, some animals have also displayed a decrease of their densities following the hurricane, like some snails and walking sticks [34]. The impact of hurricanes on lizards has received only little attention. McCoid [21] has noted cumulative effects of typhoons suggesting a resilience to storm influences by atoll-dwelling reptiles. He has brought to light that typhoons have felled an unknown but large number of trees on Cocos Atoll in the Mariana. An estimation of 40–60% of *Casuarina equisetifolia* have been lost cumulatively during two typhoons in 1990 and 1991. *Emoia atrocostata* populations, a littoral-restricted skink, have declined by over 90% due to combined effects of both typhoons. Population decrease has been only observed for habitat specialized species related to the sea border like this skink and also *Cryptoblepharus poecilopleurus*. Forest species have been less negatively impacted. Reagan [35] has noticed a clear density decrease for *Anolis* lizards after the Hurricane Hugo in Puerto Rico. This has been explained by canopy destruction leading to hotter and drier conditions near the ground level within the forest. A different response to habitat destruction has been observed based on species. The main conclusions ensuing from all studies on Hurricane Hugo in Puerto Rico have shown that hurricanes may be the most important factor controlling species composition and some aspects of ecosystem dynamics in the Caribbean. Findings on birds, coupled with the frequent occurrence of hurricanes in the Caribbean, suggest that there is some pressure on bird populations in this region to maintain plasticity in habitat and dietary requirements [36], both conditions being characteristic of all widespread tropical island lizards. The hurricane has altered forest structure so much that forest composition and dynamics could be affected for many years [37]. Future field work should focus on a better understanding of lizard dynamic related to typhoons in the Pacific, particularly of geckos which are dependent on trees, mostly dead trees engendered by typhoons. However, note that the positive effect on geckos following a typhoon will only be detected long after the perturbation, once large dead trees have been dried out and their bark separated from the cambium, thus creating an available space. Consequently, studies made the year following a typhoon are not really relevant to demonstrate post-typhoon increased population dynamic of geckos.

Skinks seem to be less dependent on a hurricane-based population dynamic since they are less dependent than geckos on egg laying sites availability. However, hurricanes can have a positive impact through the increase of open habitats because the limiting factor for forest skinks should rather be related to thermoregulation site availability fulfilled thanks to mobile sun patches on forest floor. Hurricanes increase light penetration through defoliated canopies and landslides triggered by rainfall. Also, increased litterfall leads to the development of some soil nutrients and the augmentation of arthropods densities that is food for lizards. Semi-fossorial skinks could be disadvantaged according to their intolerance to desiccation but such species are uncommon in tropical island communities due to their inability to colonize islands through natural rafting [18].

5. The role of past sea level variations

A third event that should have had a significant impact on the gecko population dynamic are the important sea level variations that occurred during late Pleistocene and Holocene, about 40 000 years ago. They have sometimes reached nearly 100 meters below current sea level [38], thus completely changing the island size and shape. Sea lowering in itself has no impact on gecko population dynamic. It just allows forest to extend its range along the exposed sea areas until sea level rises again, thus giving rise to an important *salinity crisis* [38–42]. All the newly created littoral forests have slowly died. Although inland forests were located far from the sea border salt could contaminate the fresh water lens on which trees certainly depend, at least on atolls. It has brought about a huge amount of dead trees available for geckos to lay their eggs. The surface restriction has occurred during a long time (in terms of gecko generations) and progressively spread inland until current island size and fresh/salty water equilibrium have been reached. The past sea level dynamic should certainly have had a significant impact on Pacific island gecko evolution, but also on the evolution of most Pacific biota [43] including marine animals like elapid sea snakes [44].

6. Conservation perspectives

One of the main results of our observations is the perspective given to gecko studies and their conservation. As egg laying sites could be a major limiting factor for most arboreal gecko population dynamic depending on natural events 'regularly' providing them such sites (like hurricanes and typhoons, volcanism, sea level variations) and artificial historical events (garden openings in forested areas), one can expect the creation of such artificial sites to lead to a significant increase of their population dynamic. I suspect that the best way to produce such artificial egg laying sites would be to follow nature. In this way, size and shape of epiphytic myrmecophytes with numerous small cavities would certainly be the best model to follow, since gecko eggs are found in such plants. Firstly, such artificial structures probably could allow the collection of several unknown or rare forest canopy or tree trunk lizard species that depend on trees for their biology, and only rarely come to the ground level. Secondly, it would permit better knowledge of rare arboreal species like the voracious gecko *Gehyra vorax* or *Lepidodactylus buleli*, or even New Caledonian diplodactylids like *Rhacodactylus* sp., among many others [45]. Such artificial sites could experimentally permit to test quantitatively the assumptions I have made in that paper, mostly based on field observations waiting to be tested experimentally. Eggs and specimens could be marked and their incubation and activity, respectively, be followed during time in and around the artificial shelters. These artificial shelters, placed high on tree trunks, could be regularly inspected by a mechanical system with easy access, even if placed high in trees or even on the canopy. Finally, it would allow increasing rare gecko densities in selected areas like natural reserves and parks. Thanks to the use of a tool such as artificial egg laying sites and shelters for geckos, ecotourism could benefit from having an easy way to show the visitors rare arboreal geckos and their eggs (e.g., like *Uroplatus* geckos in Madagascar). One could even imagine killing occasionally some large trees, choosing particular species providing abundant loose bark when dead. In the same way, the creation of artificial refugia made of a crumbly substrate has been suggested on the Mascarenes in order to limit future disturbances by the introduced aggressive gecko, *Hemidactylus frenatus*, on terrestrial endemic *Nactus* populations [46].

7. Egg laying sites availability and natural versus Man-mediated island colonization

Eastern Pacific island reptiles are often considered as having been recently introduced by man, and their genetic uniformity and abundance in and around man-made habitats are used to prove this [2,8,10,47,48]. However, natural rafting certainly occurred in the past, long before human arrival on those islands. Observations attesting to such natural colonization exist and are not exceptional [49–56]. Schoener and Schoener [57] have called such typhoon-mediated movements a '*pulse-like immigration*'. Some Pacific island lizards have a large distribution that encompasses most of the tropical Pacific. While making genetic analysis of their population at a large geographical scale, their genetic uniformity is most often strikingly evident but note that most techniques would not distinguish 200 vs. 10000 years old established populations. Such a genetic uniformity has also been demonstrated recently concerning the first human colonists of the Polynesian Pacific islands who too had elaborated efficient ways to fight against isolation through numerous and easy inter-island travels [58]. I suspect this homogeneity in most widespread island lizards to be related to their specialization rather than to a recent man-mediated introduction. I consider them as ecological generalists biogeographically specialized for the colonization of the most remote oceanic islands, first by natural rafting and secondary indirectly by human transportation. They present many adaptations to inter-island travel [18], like the first human occupants, and no population can be genetically isolated. Thus, constant inter-island gene flow should be a significant barrier to prevent any local speciation. In the same way, all 10 helminth parasite species found in 11 species of separate Pacific island *Emoia* skinks are generalists (they parasitize several different hosts), thus clearly increasing their dispersal success on these islands [59]. Regarding the most remote eastern tropical Pacific islands, populations are more subject to local evolution through increased genetic separation from other conspecific populations. This is the case on Easter Island where the population of a widespread skink is considered as an endemic subspecies, *Cryptoblepharus poecilopleurus paschalis*, morphologically separated from the western Polynesian populations [60,61]. Similarly, on Clipperton Atoll, populations of *Emoia cyanura* clearly show significant morphological, ethological and ecological differences when compared to western related populations [62], also justifying their subspecific status.

Most of these Eastern Pacific widespread lizard species are often present inland but all of them live on the sea border, thus being easily transported from one island to another during typhoons. Typical forest gecko species from eastern Melanesia (like geckos genus *Nactus* or *Gehyra vorax*), or larger forest skinks genus *Emoia* (e.g. *Emoia samoensis* group species) or a small forest skink (*Emoia caeruleocauda*) are absent from the area east of the Cook Islands and north on Hawaiian Islands. This lack is not explained by human transportation hazards but rather because their natural habitat is linked to humidity needs (closed forest), which are not available during natural inter-island travels, in addition to the large size of some of these species which does not allow them to tolerate restricted-food intake as smaller species do. Most of the unoccupied Eastern Polynesian islands are, however, in accordance with their habitat requirements. Thus, distributional and genetic homogeneity of many widespread island lizards cannot be considered as demonstrating their recent arrival through man-mediated transportation. Moreover, the most recent studies seem to show that natural dispersal is an important and frequent event and that its implication in species distribution has been overlooked in the past [63–70]. Eastern Pacific island lizards have certainly undergone spectacular dispersal adaptations allowing only rare opportunities for populations to be isolated from the gene flow at the origin of their wonderful biogeographical success story, later reproduced in the same way . . . by the Polynesian settlers.

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