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# Lizards and rodents: an explanation for their relative species diversity in Chile

## Lagartijas y roedores: una explicación para su diversidad relativa en Chile

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It is discussed that the relative richness of lizard fauna in Chile might be related to ecological attributes of this group (marked altitudinal segregation, coarse-grained habitat selection, and low vagility associated with ectothermy), which would favor a rapid speciation pattern concomitantly with Quaternary Glaciations.

Lizards would diverge on mountaintops during interglacial periods and would merge into fewer forms or further diverge on the lowlands during glacial periods' intermingling. It is shown that number of subspecies per species in mountaintops is greater than on lowlands, which is consistent with the above hypothesis hereafter referred to as "mountain speciation mode". However, it is also documented that lizards might exhibit a "valley speciation mode", in which case they would diverge in non-icy valleys during glacial periods, intermingling with lizards in adjacent valleys during interglacials. As in the previous case, merging or speciating of divergent forms would depend on the degree of reproductive isolation attained.

As a contrast, it is discussed the situation of the relatively poor Chilean rodent fauna. It is shown that although rodents exhibit some altitudinal segregation they do not form more subspecies on mountaintops than on lowlands, which is possibly related to their fine-grained habitat selection and greater vagility associated with endothermy. On the other hand, number of subspecies per species is positively correlated with the extension of its geographical range, which strongly suggests a "valley speciation mode" for rodents in Chile.

SPECIATION BIOGREOGRAPHY QUATERNARY GLACIATIONS VERTEBRATES CHILE

## THE PROBLEM

Chile has a geographically isolated position in South America. The high Andes on the east, the barren Atacama desert on the north, and the Pacific Ocean on the west, are all strong barriers to the dispersal of most organisms (1). Concomitantly, the Chilean fauna tends to be relatively depauperated when compared with the fauna of an area of similar climate and resources, like California for example.

Mammals, ants and bees are about half as diverse in Chile than in California (2). Birds and frogs are about the same, but lizard species are about one and a half times more numerous in Chile than in California (2). In fact, speciation in Chilean *Liolaemus* species has been strong enough to produce a mosaic of alternative communities in central Chile (3). On the other hand, endemism in mammals, ants, and bees also tends to be high (1, 2, 4).

The question we will attempt to answer is why Chile seems to be comparable to an isolated but complex archipelago with copious speciation for lizards, and more like an island for other groups.

Possible explanations for differences in the number of species between Chile and California could be related to the amount of time the different groups have had to speciate in Chile, or to different resource availabilities in the two regions. However, recent studies (2, 5, 6) have shown resource supply for several groups of organisms is quite comparable in Chile and California. On the other hand, paleontological evidence is weak or inexistent, and therefore does not aid to explain the patterns. It is conceivable though that both of these factors could be shown to be important.

In this contribution we have taken an alternative route which we hope will at least offer a partial explanation for the relative species diversity phenomenon. We will attempt to show that ecological differences between lizards and other groups, manifest themselves in different speciation patterns. Because available ecological information about most taxa is scarce, we will restrict ourselves mostly to the comparison of lizards with rodents. There is no doubt that these are "particular" groups, but as will be seen later in this paper, their speciation modes could offer clues for future work on other taxa.

First we will document, in a fairly detailed manner, the ecological attributes of lizards in relation to their proposed pattern of speciation. We will then compare these attributes with the available ecological information on rodents and their postulated speciation mode.

## ALTITUDINAL PARTITIONING

Chile is basically a mountainous country. The high Andes border its east side, and on the west coast it is limited by the Coastal Ranges, with only a narrow central valley in between. This physiography is strongly reflected in the distribution of the organisms. Thus, Chilean lizards tend to exhibit strong altitudinal partitioning. Of the 36 *Liolaemus* species known in Chile, 20 are predominantly found above 1000 meters above sea level (masl), and only 3 of them are known to live above and below this altitude. However, at different latitudes altitudinal segregation varies. Between aproximately 18° and 27° latitude south by the Atacama desert, there are 8 *Liolaemus* species above 1000 masl and only 1 below it. Further south, as the valley gets more mesic, the proportion of species found below 1000 masl increases monotonically. Between 27° and 37° latitude, the ratio of species above 1000 masl to species below is about 1.6; between 37° and 42° latitude, the ratio is 1.0, and further south it is 0.0. This trend reflects the low productivity in the northern valley, the more mesic climate in the central part, and the low average height of the Andes south of 42° latitude (see 7).

Thus, there is strong altitudinal partitioning only in the central part of the country, roughly around Santiago. Fig. 1 shows altitudinal species sequences on the mesic Coastal Ranges (El Roble, La Campana) and on the drier Andes slopes (Lagunillas). The figure starts only at about 1000 masl and does not contain the species below the level (see 8). Still, it can be seen that there is species turnover on the three mountains, although it is not strictly parallel in all of them.

It is important to emphasize at this point that in other transects covering a wider altitudinal range, some species would probably be added, and perhaps other be dropped, depending on slope and exposure. The important aspects in Fig. 1 are the existence of species turnover and the lack of parallelism in the distribution of species on nearby mountains.

The biological reasons for the altitudinal species replacement are currently being investigated, but there are already some emerging patterns. Some species in Fig. 1, like *L. nigroviridis* and *L. leopardinus* are typically high-mountain lizards, whereas other species like *L. tenuis*, *L. schroederi* and *L. nitidus* are low altitude species further south or north (8, and personal observations). Species would thus be "tracking" in altitude and latitude conditions where they can survive and reproduce. However, what are the restrictions which limit the use of the whole altitudinal gradient by the species?

Fuentes and Jaksić (in preparation) show that density of grasses can impose a strong selective pressure on lizards, such that grass and open ground analogue species can be distinguished. Optimal morphologies for survival in each habitat are different, and thus presence or absence of grass acts as a sieve separating true alternative communities (9, 10) in each environment.

We found this mechanism to explain some latitudinal as well as altitudinal habitat partitioning. Thus, *L. nigroviridis* is preferentially a rock dweller, but can frequently be found on the ground if grass density is low. At Lagunillas (east of Santiago) we found that *L. leopardinus* replaces *L. nigroviridis* as grass density increases. Both species are preferentially rock dwellers, but have the option of hunting on the ground, and *L. leopardinus* is more of a grass-species than *L. nigroviridis.*

The same grass-non grass phenomenon could be involved in setting an altitudinal limit on *L. lemniscatus* (Fig. 1). *L. lemniscatus* is a grass-species which uses ground preferentially (5, 11). At El Roble, as grass density decreases with altitude, *L. lemniscatus* drops out of the community, being replaced by the juveniles of *L. nigroviridis* (see 5). In this case *L. leopardinus* is absent from the Coastal Ranges.

Other species seem to be strongly associated with the presence or absence of a very particular environmental feature. Thus, *L. monticola* is a rock dweller strongly associated with the presence of boulders and rocks (8, 11, 12). These features tend to be more frequent high in the mountains, close to tops and ridges, and concomitantly *L. monticola* drops out of the community at low altitudes. Similarly, *L. tenuis* is a tree dweller (5, 8) and its presence is strongly associated with the distribution of trees.

Besides these particular elements, some general metabolic difficulties seem to add more constraints on high altitude species and to enhance zonation. Shortening of the growing

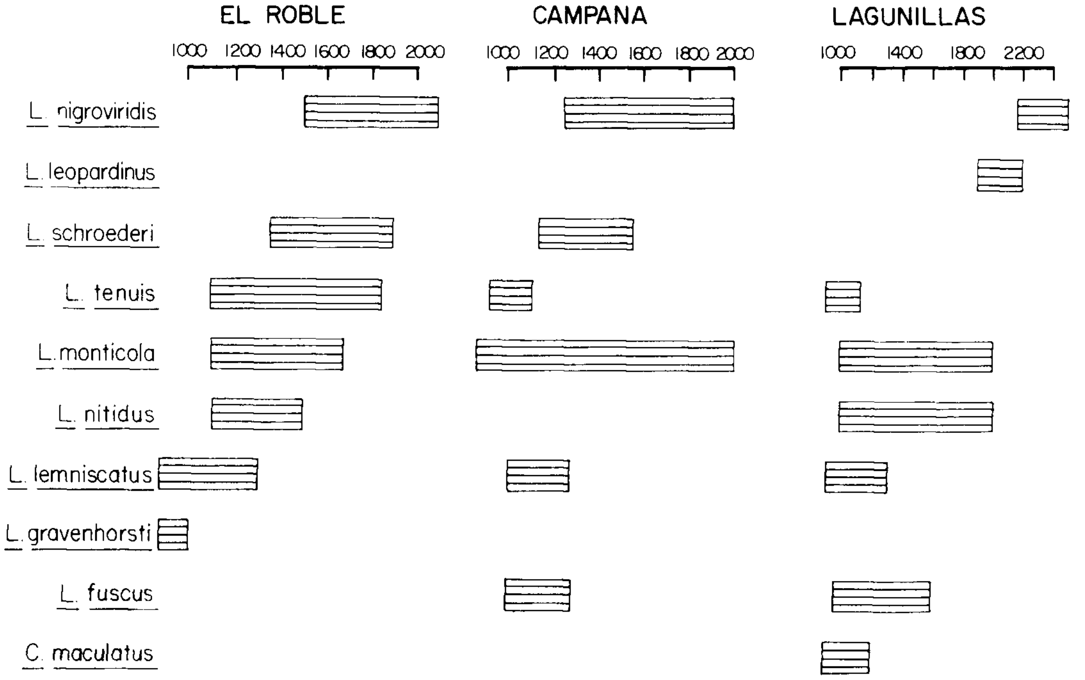

*Fig. 1. Altitudinal species replacement of lizard species.*
Altitudinal species sequences at the closeby mountains El Roble, Campana, and Lagunillas are compared. Data for El Roble were obtained from Pinto *et al.* (43). Data for Campana from Jerez and Ortiz (44). Notice that species sequences differ on the three mountains. See the text for further explanation and discussion.

season with altitude imposes strong restrictions on some species. Fuentes and Di Castri (13) noted that high altitude *Liolaemus* species are forced to be omnivorous, incorporating vegetable tissues into their diet. They interpreted this plant consumption as compensation for low and unpredictable insect densities in those environments. Furthermore, Fuentes (5) found that large *Callopistes maculatus* eats vegetation at its limit of altitudinal distribution, but not further down. Again, it was suggested that as favorable season shortens with altitude, lizards have to be less insectivorous and have to compensate the low consumption of insects by eating plant material. The problem is that only large lizards can use vegetation efficiently, and not all plants are edible (13, 14). Besides the physiological difficulties for most lizards of eating low caloric plant material (15, 16), high altitude *Liolaemus* also tend to be viviparous (8, 17). This indicates that shorter favorable seasons at higher altitudes could impose altitudinal restrictions to egg development of some *Liolaemus* species. On the other side, low altitudinal limits are likely to be associated with particular habitat features (i.e. rocks and trees), and diffuse competition (9) in these more stable environments.

In sum, in central Chile there is altitudinal species turnover of lizards and this pattern seems to be associated with alternative morphologies and behavior of the species. In general, species with optimal fitness at one point in the altitudinal gradient are not equally adapted to other habitats, suggesting the presence of ecological barriers to lizard movement between mountains.

## MOVEMENTS BETWEEN MOUNTAINS

Hellmich (12, 18) noted that high altitude species tend to diverge more than species inhabiting the valley. In fact, using the data by Hellmich (12) and Donoso-Barros (8), we have been able to show that species living under 800 masl tend to have fewer subspecies than species above that level (Fischer's exact probability test, $P<.001$). Furthermore, species living above and below 800 masl *(L. nitidus, L. fuscus,* and *L. lemniscatus)* do not form subspecies. There are two types of exceptions to this rule:

1. Species which live on mountains and do not form subspecies. However, this is strictly not an exception but sustaining evidence, since these species are known from only one locality and therefore give strong evidence for genetic isolation on mountaintops. Species in this category are *L. signifer, L. ornatus, L. mocquardi, L. pantherinus, L. fitzgeraldi, L. lorenzmulleri, L. buergeri, L. kriegi, L. paulinae, L. constanzae,* and *L. darwini* (see 8).
2. Mountain species at high latitudes do not form subspecies. However, at high latitudes mountains are very low, and distinction between mountain and valley becomes arbitrary (see 7). Again, this is expected from the hypothesis and does not contradict it. Species in this category are *L. magellanicus, L. kingi, L. lineomaculatus, L. d'orbignyi,* and *L. fitzingeri* (see 8).

Thus, the pattern of divergence on mountains but homogeneity at low altitudes, confirms the suggestion based on ecological data regarding isolation of lizard populations living at high altitudes. As we saw before, habitat selection (most likely in relation with interspecific competition) can set barriers to movement of lizards on an altitudinal gradient. It is likely then that these barriers have allowed for intraspecific differentiation in mountain species (see Fig. 2).

Interestingly, the degree of differentiation between mountain populations has been comparable to, or greater than differences observed between mainland and island populations. There are no island species absent from the mainland, and the existing island forms are only subspecies of mainland species (8).

Here we refer only to islands connected with the mainland during the last glaciation, that is separated from the continent by at most 100 meters deep channel (19, 20). This restriction excludes mainly the Juan Fernández archipelago and some large islands on the southern channels, both of which are not known to have lizards. It also excludes Easter Island, since it is oceanic. Typical island subspecies are *L. cyanogaster brattstroemi, L. pictus chiloensis, L. pictus major* on the southern Chiloé archipelago (43° latitude south), *L. nigromaculatus ater,* and *L. nigromaculatus sieversi* at about 30° latitude.

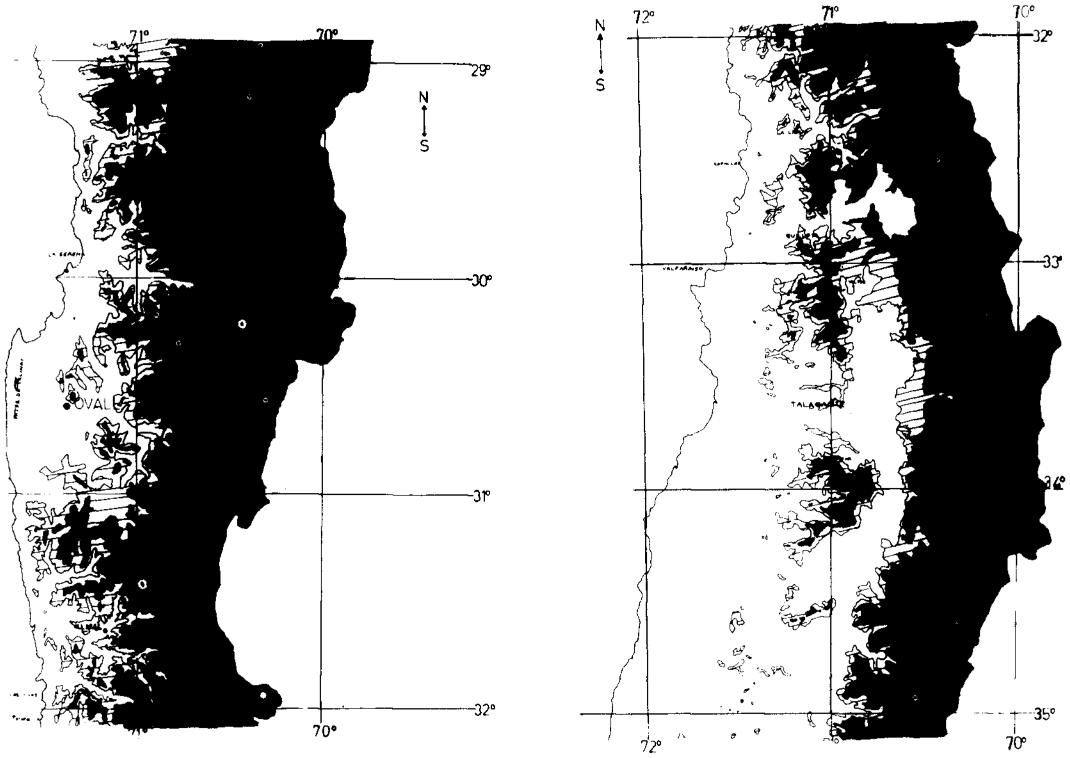

*Fig. 2. Altitudinal islands in central Chile.*
Distribution of heights above 1000 masl (black) or above 600 masl (dashed) are comparable to an altitudinal mainland on the east, with an archipelago on the west. Glacial snows could have been as low as 900 masl (see 21) and therefore the density of altitudinal islands is a measure of alternative recolonization opportunities in central Chile during interglacial times. See the text for discussion and more explanations.

In sum, adaptations of lizards to their habitats seems to be fine enough to entail reproductive isolation between populations on nearby mountains.

### A TWO WAY SPECIATION MODEL

Based on research in the European Alps, Hellmich (12) suggested the Andean races of *Liolaemus* would develop on different mountains during interglacial periods and eventually come into contact with each other during glacial periods. That is, as snow level approaches lower altitudes, high altitude lizard species and subspecies would shift their distributions closer to the valley, with many of them coming in contact with each other. If reproductive difference achieved during the isolation in the interglacial period were pronounced enough, natural selection would have favored resource partitioning and hence new forms capable of coexistence.

By the above mechanism, races and perhaps species formation would follow interglacial isolation on separate mountains. During glaciations, populations formerly on different ranges would intermingle and further diverge, or if differences achieved are not strong enough, they would merge into one species. At any rate, this is a speciation model which in repeated glaciation events could generate great diversity.

In central Chile there have occurred three to four glaciations (21) and there are separate ranges along the Andes, as well as in the Coastal Ranges (7), thus allowing for multiple species formation within even a small latitudinal range. The essential factors in this speciation mode is that species partition the habitat altitudinally and that during interglacial periods, movements between mountains are restricted and comparable to movements between mainland and islands on the continental shelf. In the remaining part of this contribution we shall refer to this speciation mode as "mountain speciation".

A second mode of speciation, not exclusive of the former, is also likely to have operated in Chile. During glaciations, pockets of non snowed habitats or at least with short growing seasons, have been inferred to occur in the southern Andes (21). These pockets being more or less isolated from each other, can lead to reproductive isolation between populations. During interglacial periods, the formerly isolated populations would intermingle and further differentiate, or merge into fewer forms. For analogous reasons as before, we will refer to this speciation mode as "valley speciation". In valley speciation, the essential features are restricted movements between valleys or pockets during glacial periods, and mixing during interglacial periods.

Fig. 3 shows the two speciation modes in a diagram. Note that for three mountains and two valleys, as shown in Fig. 3, each cycle of mountain speciation would at most triple the number of species (species 1 and 2 in Fig. 3). On the other side, the same design operating by valley speciation would at most double the number of species per cycle. The point is that speciation rate depends directly on number of isolates and amount of intermingling. Clearly, speciation rate of groups using both speciation modes would be considerably higher than speciation rate of groups using only one mode.

For all the reasons given above, lizards seem to fall into the mountain speciation mode. The evidence given on their altitudinal stratification and on the isolation between mountains, with presence of subspecies and even species on some mountains during the present interglacial, point in this direction. However, in addition lizards could have also used the valley speciation mode. Unfortunately, since we are living on interglacial period at present and therefore during an intermingling phase for valley speciation, it is not possible to clearly determine its importance.

Possible examples of valley speciation in lizards could be the geographical subspecies patterns of *L. platei* and *L. nigromaculatus*. *L. platei platei* is roughly distributed between 26° and 32° latitude south, whereas its only known subspecies *L. platei curicensis* is restrict-

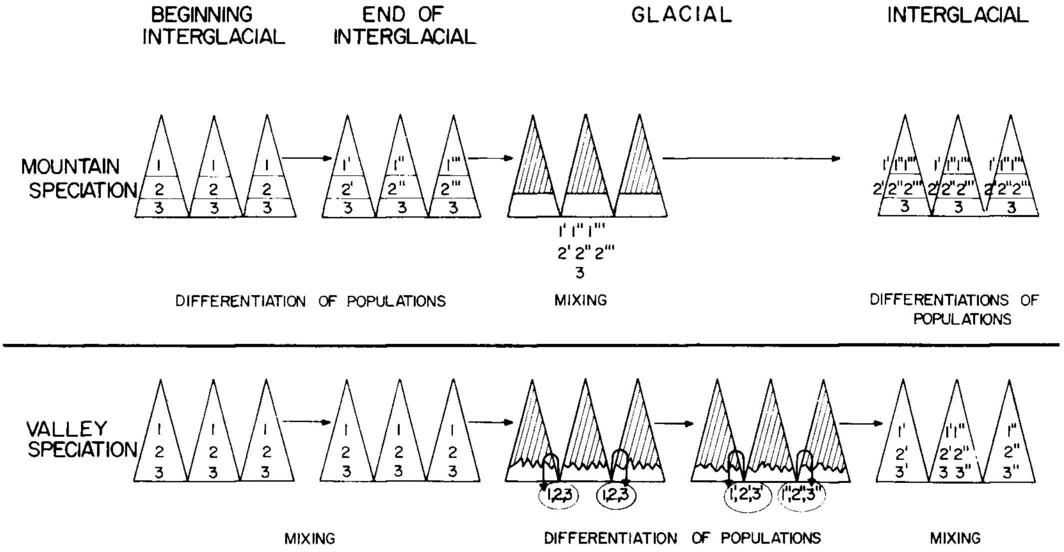

*Fig. 3. Speciation modes.*

Mountain and valley speciation are asynchronous with regard to the phases of differentiation and of mixing of differentiated populations. In mountain speciation, differentiation occurs during interglacial periods and mixing in valleys during glaciations. The opposite is true of valley speciation, where differentiation occurs in isolated habitat pockets or valleys during glacial periods. See the text for further discussion.

ed to a few valleys of Curicó, at 35° latitude (see 22). Both Donoso-Barros (8) and Muller and Hellmich (22) insist on the subspecies level of differentiation, although this is not crucial for the argument. It is reasonable to assume *L. platei* once had a wider distribution, covering the gap between 32° and 35° latitude south. During the last glaciation, the previously continuous distribution of *L. platei* could have been fragmented. Later, during the interglacial, *L. platei* would have persisted only in its known distribution, with extinctions between 32° and 35° latitude. Here, competition with other *Liolaemus* species could have been very important, since they reach high species densities in that latitudinal range (8). Fuentes and Jaksić (in preparation) offer evidence suggesting that *L. platei* — a non grassy species æ is in fact replaced by *L. lemniscatus* — a grassy species — at about 32° latitude south. On the other hand, the permanence of *L. platei curicensis* since the last glaciation is not clearly understood, but could be related to the local physiography.

The second evidence for valley speciation in lizards is the kreiss of *L. nigromaculatus*. *L. nigromaculatus* and its numerous subspecies, form a latitudinal cline (2, 12), suggested to be a manifestation of secondary contact (12). Interestingly, the discussed *L. platei* — *L. lemniscatus* transition occurs at about this same latitude (32°) and shows clear signs of hybridization and secondary contact (Fuentes and Jaksić, in preparation). It is very likely therefore, that there was a glacial barrier to dispersal at about that latitude. Nowadays we would be observing the merging and differentiation of formerly isolated populations. More evidence on areas of secondary contact, and knowledge of which valleys were glaciated (see 21) are needed before we can postulate a set of barriers to dispersal in the past.

Rodents present a clearly contrasting situation in comparison to lizards. Rodents exhibit altitudinal habitat partitioning (see 23, 24, 25, 26) but, as will be seen, also more movement between mountains. Fig. 4 shows the patterns of altitudinal segregation at about 18° latitude south, and Malleco (39° latitude). It can be seen that in both situations there are species restricted to mountain tops, and species living further down.

Cody *et al.* (2) used beta-diversity, that is species turnover over comparable habitat transitions, to describe species turnover of mammals and lizards in California and Chile. They found that beta-diversity on altitudinal transects is quite comparable for rodents and lizards in central Chile. This means not only that lizards and mammals change with altitude, but that in central Chile — at least around the latitude of Santiago — they seem to change at about the same rate.

The biological compromises involved in the altitudinal segregation by rodents are not as clear as in lizards. In North America, structural habitat (27, 28, 29) and productivity (30, 31) have been invoked in relation to habitat partitioning, but about the Chilean situation there is no published information.

Whatever the reasons are which explain the altitudinal partitioning phenomenon in rodents, one requirement of mountain speciation is not met by these vertebrates. Whereas lizards living on different mountaintops tend to be relatively isolated, the same is not true for rodents. Our evidence for isolation of lizards is the greater race formation between mountaintops than between localities in the valley. For rodents, we used data by Osgood (1) and Miller and Rottmann (32), and found this difference not to be statistically significant (Fischer's exact probability test, $P > .34$). That is, species restricted to low altitudes tend to form as many subspecies (or to be as isolated) as species living on mountaintops.

The above result is particularly important for our speciation model, since the three mammalogically better known islands off the coast of Chile (Tierra del Fuego, Chiloé and Mocha) were all connected to the mainland during the last glaciation (21), and nowadays they exhibit subspecies of mainland forms. Tierra del Fuego has three subspecies, Chiloé four, and Mocha three (see 1, 32).

The evidence suggests then, there has been time for rodent subspeciation on mountains, as well as intermingling of populations during the present interglacial, and hence the lack of differentiation.

This difference in mobility between lizards and rodents is likely to be related to their mode of thermoregulation, and energy requirements.

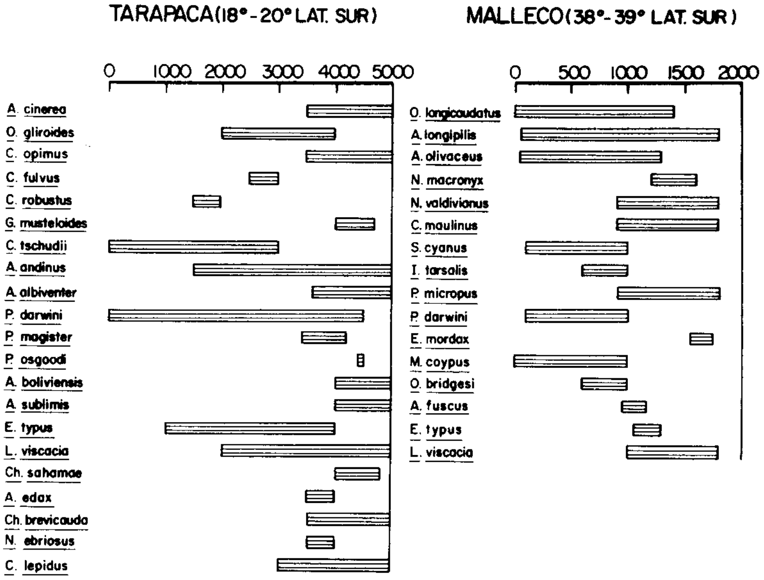

*Fig. 4. Altitudinal species replacement of rodents species.*
Altitudinal species sequences in central Chile (Malleco) and northern Chile (Tarapacá). Data for Malleco were obtained from Greer (24). Data for Tarapacá were taken from Miller and Rottmann (25), Spotorno (26), and records of Museo Nacional de Historia Natural (Chile). See the text for discussion.

Rodents are endotherms and do not have the capability to hybernate, at least in Chile (1, 24), so they are more likely to periodically shift their altitudinal range and diet. In contrast, lizards are temporal opportunists, have relatively lower energetic requirements, and restrict their activity to the season of maximum productivity, not shifting in altitude. In the sense described by Levins (33), lizards would be coarsely grained and use one environmental type preferentially, whereas rodents would be more finely grained tending to use more environmental types, related to the proportion of their occurrence. Rodents, being less specialized than lizards, would have exhibited more between-year intermingling and greater transition probabilities between mountains, and hence less subspeciation than mountain lizards.

In sum, rodents do not comply with the requirements for mountain speciation because of their high mobility during interglacials. On the other hand, rodents seem to have speciated in the valley mode. Number of subspecies of rodents is significantly correlated with breadth of geographical distribution measured in degrees ($r = .82$, $P < .0001$). That is, species distributed over long latitudinal stretches tend to have more subspecies than more restricted ones. This is evidence (certainly not conclusive) for valley isolation during glacial periods, and secondary contacts during interglacials.

In conclusion, our evidence points towards a two-mode speciation for lizards, but a valley speciation mode for rodents. In agreement with this is the fact that Chile has more lizards than California, whereas the opposite is true for rodents. The former would speciate faster than the latter, and would thus have been able to compensate for the more diverse centers of origin of the California fauna. Rodents, on the other hand, depending on more stringent speciation conditions, would have speciated at a slower rate and would therefore not have been able to compensate for the diversity of centers of origin in the Californian rodent fauna.

The by now well known radiation of altiplano rodents (23, 26, 34) would thus be linked to the existence of numerous valleys and surrounding mountains, which would have provided during glacial times the reproductive isolation needed for speciation. The geographical and ecological proximity of these valleys during the interglacials, their isolation from each other by the high mountains, and the vaster areas associated with the altiplano, would have provided the conditions for greater speciation of rodents in the northern region than in the more extended southern Andes.

Other groups besides rodents and lizards are more difficult to explain, and we do not have the required information to examine their speciation patterns. However, it is possible that both birds and frogs also have valley speciation patterns. Birds have high mobilities and are not expected to show the large phenotypic differences between mountains as lizards do. Cody (35, 36) has shown Chilean birds tend to segregate more by regions than by habitat types. Speciation in these animals would probably operate not only between valleys, but between distant and isolated ones. Vuilleumier (37) postulated that the *Nothofagus* bird fauna associated with forest speciated phyletically, which strongly suggests that long distances are required for genetic isolation in these animals.

Birds would thus be expected to exhibit relatively lower endemism than lizards or rodents. The similarity of California and Chile bird faunas remains to be explained, but it is probably a compound phenomenon with local speciation and relatively more immigration from distant localities.

Frogs might have speciated locally (38) and could exhibit valley and perhaps some mountain speciation. Frogs seem to comply with the low mobility requirement, but to our knowledge it is not known how much altitudinal stratification they exhibit. It is suggestive though that total species counts for California and Chile frogs are about the same (see 39, 40). More research on this point is necessary.

## CONCLUSIONS

It has been assumed — and there are good reasons for it — that Chile and California offer resources for comparable faunas (41, 42). However, whereas California has received immigration of species from centers in the north (Great Basin), south and southwest (Sonoran and Mexican deserts), the Chilean immigration has been relatively low. For several faunistical groups, speciation in the country has been copious. Among these, lizards *(Liolaemus)* seem to be an excelent example of adaptive radiation. Their speciation has been explained as a result of the greater speciation rate as compared to other groups, particularly rodents. The basic difference between these two types of vertebrates seems to reside in their different mobilities, ultimately related to their endothermy or ectothermy. As a consequence of this difference, lizards would speciate during and between glaciations, whereas rodents would do so only during glacial periods. It is possible the speciation of birds and frogs could be explained by the same scheme.

## RESUMEN

Chile es un país relativamente rico en lagartijas, pero pobre en roedores, en comparación con lugares que exhiben características similares de clima y recursos. En este trabajo se intenta responder por qué nuestro país ha sido análogo a un archipiélago para las lagartijas (alta diferenciación específica e intraespecífica), pero más bien como una isla para los roedores (menor diversidad y diferenciación intraespecífica).

Se muestra que las lagartijas exhiben una fuerte segregación altitudinal, que es particularmente patente en la zona central de Chile (véase Fig. 1). La razón para este reemplazo altitudinal de especies estaría relacionado con la selección de ciertas características del hábitat por parte de las lagartijas, que les proporcionarían condiciones óptimas para su sobrevivencia y reproducción. En el texto se analizan numerosos casos en que esta situación es evidente.

Intimamente ligados a la selección del hábitat se encontrarían las morfologías y el comportamiento de las lagartijas, por lo que fenotipos óptimos en un cierto lugar no lo serían en otro, en donde podrían ser reemplazados por fenotipos (especies) diferentes. La estrecha relación que existiría entre fenotipo y ambiente seleccionado, determinaría la partición altitudinal del gradiente de hábitats en las montañas, restringiendo el flujo de individuos desde ciertas porciones del gradiente (en las cuales constituyen el fenotipo

óptimo) a estratos similares en montañas cercanas.

Este razonamiento basado en datos ecológicos, se ajusta al hecho que las lagartijas que están restringidas a las montañas muestran mayor divergencia (mayor cantidad de subespecies) que aquellas que viven en el valle. El mayor aislamiento de las cumbres habría entonces permitido la mayor diferenciación intraespecífica que se observa en las montañas. En este sentido, las regiones montañosas se asemejarían a un conjunto de islas en las cuales se puede producir divergencia intraespecífica, debido a la restricción del flujo de individuos entre aislados continentales (véase Fig. 2).

Anteriormente se ha sugerido que las razas de *Liolaemus* se desarrollarían en montañas durante los períodos interglaciales, entrando en contacto con otras razas similares cuando el descenso de la nieve (durante los períodos glaciales) las empujara a bajar al valle. En esta situación, o se refuerzan los mecanismos de aislamiento reproductivo, o las especies incipientes se refunden en una sola. En Chile han habido tres o cuatro glaciaciones, de manera que el mecanismo de especiación propuesto podría generar gran diversidad en sucesivas recolonizaciones de las montañas. Los factores esenciales en este modelo de especiación requieren de la partición altitudinal del hábitat en las montañas, y la restricción del movimiento de poblaciones que viven en distintas montañas durante los interglaciales. A este modo de especiación, los autores llaman "especiación en montañas".

Un segundo modo de divergencia filética podría también ocurrir durante la alternancia de períodos glaciales e interglaciales, pero a través de "bolsones" o valles libres de hielo que quedarían aislados unos de otros, permitiendo así la diferenciación de las poblaciones. A este tipo de especiación, los autores llaman "especiación en valles". Durante los períodos interglaciales, las poblaciones previamente aisladas podrían reunirse y divergir aún más, o refundirse en una sola especie. Los dos tipos de especiación propuestos se ejemplifican en la figura 3.

En base a las premisas de estos dos modos de especiación, y a la ecología de las lagartijas, se postula que éstas especiarían en Chile a la manera "de montaña", aunque también se citan posibles ejemplos de especiación "de valle". La suma de estos dos modos de especiación, actuando durante sucesivos ciclos glaciales, explicaría entonces la gran diversidad de lagartijas presentes en Chile.

Como contraste se presenta el caso de los roedores chilenos, que son bastante menos diversos que las lagartijas. Se discute que, aun cuando los roedores exhiben partición altitudinal en montañas (véase Fig. 4), también presentan mayor movilidad entre ellas. A modo de apoyo a esta proposición, se muestra que los roedores de montaña no forman significativamente más subespecies que los de valle. Esto, junto a otras evidencias, sugiere que los roedores especiarían al modo "de valle".

En conclusión, los autores proponen que la diferencia en diversidad de lagartijas y roedores podría deberse a sus distintos modos de especiación: "de montaña" y "de valle" para el primer grupo, pero sólo "de valle" para el segundo.

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