Arch. Biol. Med. Exper. 12:143-152, 1979

Two types of adaptation of vertebrate predators to their prey

Dos tipos de adaptaciones de predadores vertebrados a su presa

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(Recibido para publicación el 3 de diembre de 1977)

JAKSIĆ, F.M., FUENTES, E.R., YÁÑEZ, J.L. Two types of adaptations of vertebrate predators to their prey. (Dos tipos de adaptaciones de predadores vertebrados a su presa). Arch. Biol. Med. Exper. *11*, 1978. *12*:143-152, 1979.

Two types of adaptations of Chilean carnivorous vertebrates are documented and a unifying interpretation is made by means of an economical model.

The first case reported corresponds to the situation which arises when a new potential prey item (the European rabbit *Oryctolagus cuniculus)* is introduced to a coadapted hunting set (Chilean carnivores and raptors). It is shown that predators are not adapted to hunt for the European rabbit and consequently they tend to ignore it while favoring native prey.

They second case is concerned with the extreme dietary restriction exhibited by the iguanid lizard *Liolaemus monticola,* which preys exclusively upon one genus of ants. It is shown that this lizard exhibits not only behavioral adaptations for monophagy, but also physiological ones related to the chemical composition of its prey.

Both cases are interpreted through a model in which chemical (toxicity) and physical (catchability) properties of prey are related to cost and benefit trade-off for the predator when accepting or rejecting a new item in its diet.

PREY-PREDATOR INTERACTIONS COADAPTATION ECOLOGICAL MODEL

The aim of this contribution is to document two types of adaptations of carnivorous vertebrates to their prey, and then show the relation between them by means of an economical model.

First, we will discuss the situation which arises when a new potential prey item is introduced to a coadapted hunting set. We will use data on the European rabbit *(Oryctolagus cuniculus)* recently introduced to Chile, and attempt to show that although there are predators for *O. cuniculus* in central Chile, the rabbit behaves as if they were not effective. In this case, *O. cuniculus* would be only a potential prey item.

Secondly, we will discuss the extreme dietary restriction exhibited by *Liolaemus monticola* (Lacertilia: Iguanidae). This species has been shown to specialize on only one genus of ants, namely *Camponotus.*

In the first case mentioned, predators appear not to be adapted to hunt *O. cuniculus* and consequently "skip" it, whereas in the second case, *L. monticola* exhibits extreme specialization to one class of item and neglects the others.

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AVOIDANCE OF AN EXOTIC PREY ITEM

Oryctolagus cuniculus is originally European (1, 2) but has been introduced into Australia, New Zealand, Chile, and some other countries. In Europe, *O. cuniculus* is know to restrict its activity to the neighbourhood of bushes where it can hide from its predators (3,4). On the other hand, in Australia, New Zealand, and Tierra del Fuego, *O. cuniculus* has been reported to achieve very high densities and to extend its activity pattern to the exposed zones between bushes (5, 6, 7). This change in behavior has been associated with the lack of adapted predators capable of controlling and restricting it to the predator-free areas under bushes (3, 8, 9).

A similar situation occurs with the native Californian rabbits *Sylvilagus bachmani* and *S. auduboni*. In mainland California these species are frequently preyed (10, 11, 12, 13, 14, 15) and have their activity restricted to the neighbourhood of bushes (16). However, on the small islands offshore, where in general predators are expected to be less frequent (17, 18), they are known to expand their distribution to areas between the bushes (15, 19).

Thus, when there are predators in the area, rabbits exhibit restriction in their habitat use, but in the absence of predators (Australia, New Zealand) they extend their activity to the "unprotected" zones between bushes.

In central Chile, around Santiago, *O. cuniculus* has been recently introduced (5, 20, 21, 22, 23) and, as we will show, its behavior resembles that of rabbits in Australia, New Zealand, and islands offshore California. For comparative purposes, the distribution of *O. cuniculus* feces can be used as a measure of their relative activity in the habitat (see 16). Figure 1 shows the distribution of rabbit feces found at Los Dominicos, on the outskirts east of Santiago. It can be seen that *O. cuniculus* use areas between bushes more than areas under them, in sharp contrast with the prevalent pattern in Europe (3). In other words, at Los Dominicos *O. cuniculus* behaves as if there were no predators, or at least as if their effect were negligible in relation to intraspecific competition.

We examined droppings of the fox *Dusicyon culpaeus* (N = 33) and pellets of the buzzard *Parabuteo unicinctus* (N = 56), the two most likely predators at Los Dominicos, and found that they consume the native rodent *Octodon degus* as well as other native rodents, but not *O. cuniculus*. Inspection of other sites in central Chile (5, 24, 35, Fuentes and Jaksić unpublished data) have shown similar results: *O. cuniculus* is eaten at most very occasionally by local predators. On the other side, *O. cuniculus* is known to achieve pest-densities in central Chile (5, 21, 22, 23).

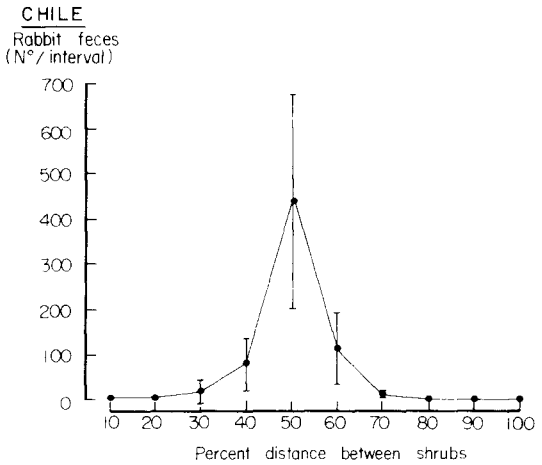

Fig. 1. Distribution of Oryctolagus cuniculus feces on the field. Percent feces found (ordinate) is shown against percent distance (abscissa) between neighbouring bushes. Notice that *O. cuniculus* at Los Dominicos tends to use the open spaces more frequently than areas under bushes. Number of feces was measured by counting scats along a transect 20 cm width joining the bushes. Mean and two standard errors around it are shown. See the text for discussion.

The pattern in Fig. 1 contrasts with the distribution of California native rabbits. Fig. 2 shows results obtained by Bartholomew (16) for the activity of *Sylvilagus bachmani* and *S. auduboni* in southern California. It can be seen that unlike in Chile, rabbits in California tend to restrict their activity to the areas under the bushes.

Interestingly, the activity pattern of *O. cuniculus* in Chile also diverges from the microdistribution of the common native rodent *O. degus*. Fig. 2 shows, on a different scale, the distribution of feces of this rodent as a function of distance from the bush. From this figure it can be seen that there is a sharp decrease in the number of feces with distance from the bush, in agreement with results obtained by Fuentes and Le Boulengé (26) and Le Boulengé and Fuentes (in prepara-

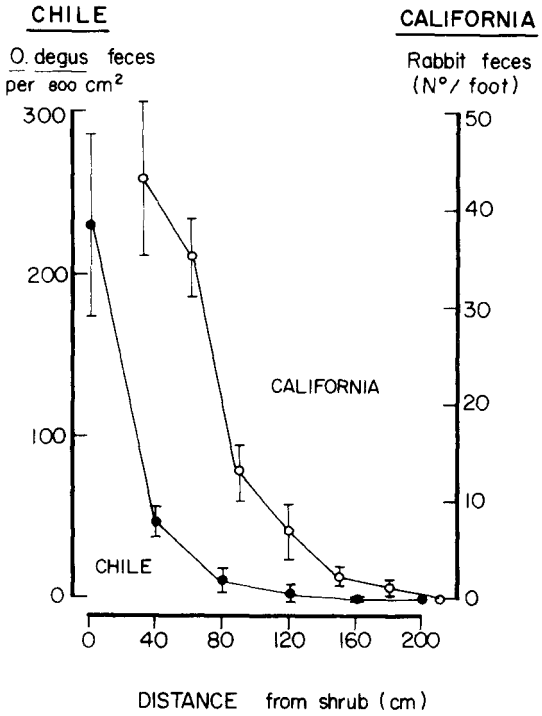

Fig. 2. Distribution of feces belonging to native animals. Feces of the Chilean rodent *Octodon degus* at Los Dominicos (left ordinate) and of native California rabbits (right ordinate) are shown against distance to the bush. In both cases the animals tend to restrict their activity to the areas close the refuge, in contrast with the pattern exhibited by *O. cuniculus* in Fig. 1. Means and two standard errors around it are shown. See the text for discussion.

tion). The same pattern is obtained when number of *O. degus* captures (corrected for the increase in the area of influence per trap, as radius increases) is plotted against distance from the bush (correlation between trappings and feces found is highly significant: $r = \cdot 99$, $P < \cdot 001$).

Fuentes and Le Boulengé (26) explained the habitat utilization pattern exhibited by *O. degus* at Los Dominicos as a consequence of predation pressure. *D. culpaeus, P. unicinctus, Buteo polyosoma,* and *B. fuscescens* are all known to eat *O. degus* (27, 28, 29, Fuentes and Jaksić unpublished data) and are quite abundant at Los Dominicos.

At this point the similarity in the pattern of *O. degus* activity in Chile and of rabbits in California should be obvious: both have restricted activities associated with effective predation (16, 26). It is the introduced species *O. cuniculus* that behaves as if it were predator-free in central Chile. This is particularly striking since there are potential predator for rabbits. Table 1 shows the rabbit predators in Europe and California, and potential ones in Chile. Inspection of Table 1 shows that for several predators in Europe or California, there are matching predators of similar size in Chile. Nevertheless, the evidence offered above suggests they are not as effective against the introduced rabbits as its original predators.

A literature survey sustains our claim: of the ten predators listed under the Chile column in Table 1, five have never been reported to eat rabbits (5, 7, 24, 25, 29, 3, Fuentes and Jaksić unpublished data). The remaining potential predators have been either reported to eat only kittens (7, 31), or the evidence for their rabbit-eating habits is mostly anecdotal (7, 30).

EXTREME SPECIALIZATION ON ONE PREY ITEM

The second case we will discuss is in some ways the opposite of the situation described above, and it refers to the predation habits of the lizard *Liolaemus monticola.* This species specializes on ants belonging to the genus *Camponotus* (Fuentes and Ipinza, in preparation), whereas other *Liolaemus* species have quite catholic insect diets without any such strong preference as *L. monticola* (34, 35, 36, 37, 38, 39, 40).

The difference between *L. monticola* and other *Liolaemus* species could be related to the chemical composition of the insects they eat. Ants are well known for their possesion of various chemical substances used as defenses or communication devices (41). On the other hand, phytophagous insects either detoxify plant toxins acting as plant defenses (42, 43, 44, 45, 46), or sequester them for their own defense (47, 48, 49). In addition, some insects synthesize chemical substances which deter their predators (50, 51). Hence, the insect fauna could actually be a mosaic of more or less toxic compounds.

Therefore, given that herbivorous insects exhibit parallel differences in degree of polyphagy and detoxicating capacity (52), it is reasonable to expect insectivorous animals to show similar trends when comparing dietary

Table 1: *Actual and potential rabbit predators*

Known rabbit predators in the Mediterranean maquis and Californian chaparral are matched by family and size with potential predators from the Chilean matorral. European rabbit predators and their measures were taken from Rodriguez de la Fuente (3.). Californian predators and their measures were obtained from Burt and Grossenheider (11), Chapman (15), Peterson (32), and Stebbins (33). The Chilean equivalents of the above species were included because of potential rabbit-eating habits evaluated by their body size, their abundance, and the habits of analogue species in Europe or California. Their dimensions were taken from Osgood (20), Goodall *et al.* (30), Donoso-Barros (31), and records of Museo Nacional de Historia Natural (Chile).

TABLE I

	Mediterranean maquis		Californian chaparral		Chilean matorral	
	Species	Head + Body Length (cm)	Species	Head + Body Length (cm)	Species	Head + Body Length (cm)
Mammals						
Canidae	*Vulpes vulpes*	60-75	*Vulpes vulpes*	56-64	*Dusicyon*** *griseus*	60-66
	Canis lupus	105-135	*Canis latrans*	81-94		
			Urocyon cinereoargenteus	53-74	*Dusicyon** *culpaeus*	70-75
Felidae	*Lynx pardellus*	80-110	*Lynx rufus*	64-76		
	Felis sylvestris	75-85				
Mustelidae	*Mustela nivalis*	25-35	*Mustela frenata*	20-27		
	Mustela putorius	31-45			*Galictis**** *cuja*	40-45
	Herpestes ichneumon	51-55				
	Meles meles	40-50				
Birds						
Tytonidae			*Tyto alba*	36-51	*Tyto** *alba*	36-38
Strigidae	*Bubo bubo*	66-71	*Bubo virginianus*	46-64	*Bubo**** *virginianus*	48-50
	Strix aluco	44-48				
Accipitridae	*Accipiter gentilis*	48-61	*Accipiter cooperi*	36-51	*Parabuteo** *unicinctus*	49-57
	Buteo buteo	51-56	*Buteo borealis*	43-61	*Buteo** *polyosoma*	45-55
	Hieraetus pennatus	46-53			*Circus** *cinereus*	40-50
	Hieraetus fasciatus	65-73			*Buteo**** *fuscescens*	68-72
	Aquila heliaca	79-84				
Reptiles						
Colubridae	*Elaphe scalaris*	160	*Pituophis catenifer*	91-254	*Dromicus*** *chamisonis*	100-150
Boigidae	*Malpolon monspessulanus*	250				
Viperidae			*Crotalus confluentis*	38-157		

*Known not to eat rabbits (5, 7, 24, 25, 29, 30, Fuentes and Jaksić unpublished data).

**Known to eat only kittens (7, 31).

***Anecdotal evidence suggests they include rabbits in their diet (7, 30).

breadth and detoxicating capacity. Species of insectivorous animals with broad diets and presumably more diverse toxins in it, could exhibit greater detoxicating capacity than more specialized species having fewer toxins in their diet.

Moreover, since vertebrates have been shown to exhibit heavier relative liver weights when subjected to toxic diets (53), insectivorous vertebrates with catholic diets would have higher liver to body weight ratios than more specialized species.

We should clarify at this point that most studies of insectivorous birds (54, 55, 56, 57, 58, 59, 60, 61) and lizards (62, 63, 64, 65, 66, 67) have assumed negligible prey toxicity. That is, it has been assumed that only a negligible fraction of the prey of these vertebrates is toxic in some degree. The only postulated constraint on insects eaten has been associated with prey size, pursue, and handling capacities.

The question we want to address is whether on the average *L. monticola* has a relatively lighter liver than other *Liolaemus* species. If this were true, the hypothesis of chemical differences in the prey, and concomitant adaptations in the predators would be sustained.

To test the hypothesis we collected specimens of eight species of *Liolaemus* (Table II). Collected specimens were taken to the laboratory, their stomach contents examined, and their oven-dry liver and body weights were calculated. Items found in the stomachs were sorted out to the order level, excepting ants which were pooled in one separate category (see 68). Diversity in the diet of each lizard species was estimated using the Simpson's index (69) on the prey categories described above.

Results are shown in Fig. 3. As expected from the insect toxicity hypothesis, *L. monticola* has a lighter liver per unit of body weight than its trophically more generalized congeners. The order level of resolution used in sorting out the prey items is too gross to distinguish between generalists's liver weights. However, more detailed identification of prey items of all lizard species could show a positive correlation. This research has not been done yet.

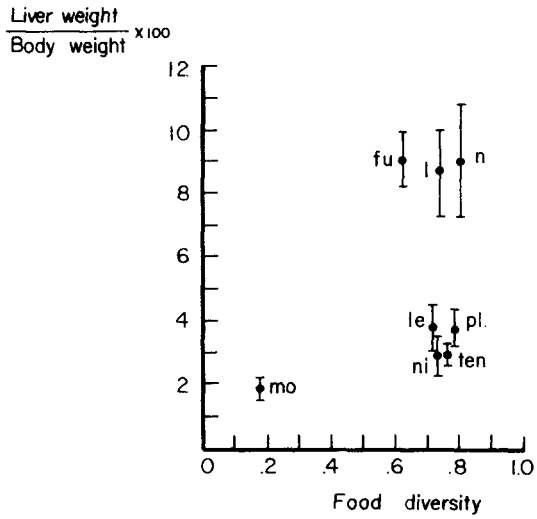

Fig. 3. Relative liver weights and diet of Liolaemus species. Liver weight as a percentage of body weight (ordinate) is shown against Simpson's diversity index for stomach contents (abscissa) in eight *Liolaemus* species. Notice that *L. monticola* has low food diversity and low liver weight, in comparison with the remaining species. In addition, there are two species groups differing mainly in relative liver weights. Mean and two standard errors around it are shown. See the text for discussion. mo = *L. monticola;* ni = *L. nigromaculatus;* ten = *L. tenuis;* le = *L. lemniscatus;* pl = *L. platei* fu = *l. fuscus;* l = *L. leopardinus;* n = *L. nigroviridis.*

TABLE II

Collection sites and sample sizes of lizards

For localities see Anonymous (79). "N" means sample size

L. monticola	N = 29	La Disputada; El Roble; Almendrillo; Cuesta La Dormida.
L. lemniscatus	N = 60	Santiago; Til-Til.
L. tenuis	N = 29	Santiago.
L. nigroviridis	N = 86	El Roble; Lagunillas.
L. leopardinus	N = 28	Lagunillas.
L. nigromaculatus	N = 65	Morrillos.
L. platei	N = 54	Morrillos.
L. fuscus	N = 43	Almendrillo; Cuesta La Dormida.

A second, unexpected result is that among generalist species in Fig. 3 lowland animals have lighter livers than animals collected on the mountains (see Table II and Fig. 3). Thus, *L. lemniscatus, L. platei, L. tenuis* and *L. nigromaculatus* were all collected below 600 m.a.s.l., whereas *L. fuscus, L. leopardinus, L. nigroviridis,* and *L. monticola* were collected between 1300 and 2000 m.a.s.l. (see also 31). This difference between groups suggests relative liver weight in generalized *Liolaemus* lizards could also be related to their needs to store energy for the winter period. Lizards are known to store energy in their tail and fat bodies (31, 70) and they could also store it in their livers. Lowland species living close to the ocean have shorter winter periods, and consequently would require proportionally less storage of energy-rich molecules in their livers than high mountain species. The livers of the latter should therefore be heavier than those of the former. Further research on this matter is necessary.

However, the most interesting result for the present purposes is the support for the insect-toxicity hypothesis, which as we mentioned earlier, could change current ideas on foraging strategies of insectivorous animals. The present evidence suggests then that *L. monticola* is exposed to a smaller variety of toxins, and would exhibit less detoxicating capacity, as measured by relative liver weight. In passing, it is worth mentioning that if the lizard diet contained relatively few toxins (as in some oligophagous insects), lizards could also sequester them as defenses. In this situation the detoxicating requirements of the specialist would be even more reduced. Further support for the insect-toxicity hypothesis will come from determination of enzymatic activity of microsomal mixed function oxydases in the liver of these animals, which is analogous to the method previously used by Krieger *et al.* (52) in lepidopteran larvae.

Thus, specialization in *L. monticola* might not only be behavioral, as is likely to be the case with potential predators of introduced rabbits, but also related to the chemical composition of the prey.

A MODEL FOR PREDATOR SPECIALIZATION

The above results can be interpreted by means of a micro-economics model (see 71). These models have been later modified and further developed for population biology by Levins (72, see also 73, 74). Here, we will apply this type of model to prey selection.

The model basically consists of two equations wich have to be solved simultaneously and the solution maximized. In our case, the first equation is for the consumption frontier (71) or fitness set (72). This equation relates the maximum grams of prey item x versus the grams of other o prey items consumed that can be detoxicated and assimilated per unit time (this equation can be plotted in the o, x plane to obtain graphical solutions).

In our model the shape of the consumption frontier will be related to the chemistry of x and o (Fig. 4). Notice that necessarily $dx/do > 0$. However, the second derivative, d^2x/do^2, is more complex (see Fig. 4). If x and o are equally nutritious and have the same detoxication difficulty, the consumption frontier will be linear. On the other hand, if the toxins x and o require that the predator be specialized, or its use requires different enzymes with long induction times, then the consumption frontier will be concave ($d^2x/do^2 > 0$). If the consumption of x or o enhances (within certain limits) the use of the other resource, the consumption frontier will be convex ($d^2x/do^2 < 0$). Enzymes with intermediate induction times could produce this type of effect.

The second equation in the model explicits the relation between pursuing and handling costs of one x or o prey item, and the caloric benefits per gram it renders. This equation represents the "indifference curves" (71) or "adaptive functions" (72). Because prey items are frequently consumed in relation to the life-span of the predator, the fitness function will be (see 72):

$$W = Px\,Wx + (1 - Px)\,Wo$$

Where W is the average fitness; Px is the relative frequency of consumption of prey item x; and Wx and Wo are the fitnesses associated with eating x or o respectively.

The optimal solution for the consumption frontier-indifference set of equations proposed, will be the one which for a given Px, Wr, and Wo

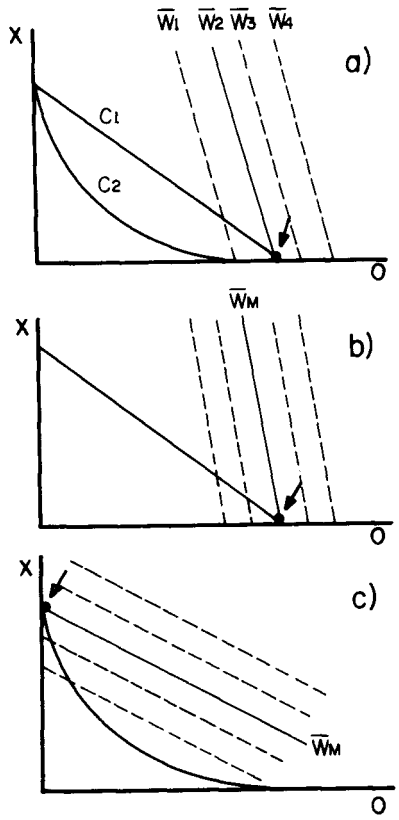

Fig. 4. Consumer choice model.

4a) C_1 and C_2 are respectively linear and concave consumption frontiers. The shape of the consumption frontier is associated with the chemistry of *x* and *o*. W_1 up to W_R are indifference functions differing in the total degree of satisfaction, or average fitness obtained. Whereas W_1 has a lower than possible average fitness, W_4 is not achievable. The optimal solution is given by the intersection of W_2 and the consumption frontier (arrow). The slope of the indifference functions is associated with the difficulty in pursuing and handling prey *x* in relation to prey *o*.

4b) Represents the optimal choice of predators in the exotic prey item situation of *O. cuniculus*.

4c) Represents the optimal choice in the *L. monticola* versus ants situatión.

See the text for further explanations.

maximizes *W* (see, 71, 72, and Fig. 4a). The problem now is to determine *Px*. We will assume the predators search for food and therefore *Px* will depend only on the time invested for clasing plus handling plus digesting (see 75). It is reasonable then to assume that:

$$Px = \frac{1 - tx}{tx + to + ts} = \frac{to + ts}{tx + to + ts}$$

Where *tx* is the average time to pursue and handle 1 gram of *x* item; *to* is the same average time to pursue and handle 1 gram of *o* item; *ts* is the search time for all, which should not depend on the prey item finally chased (see 75).

Thus, probability of attack is inversely related to costs of pursuing plus processing the prey (see 76, 77, 78, 65, 66). Hence:

$$W = \frac{(to + ts)\,Wx}{tx + to + ts} + \frac{tx\,Wo}{tx + to + ts}$$

This means (see Fig. 4a) that the higher the absolute value of $\partial Wx/\partial Wo$, the more of non-*x*, that is *o*, items will be consumed. Conversely, if $\partial Wx/\partial Wo$ is small, *x* will be preyed upon more frequently. In our case:

$$\frac{\partial Wx}{\partial Wo} = \frac{-tx}{to + ts} \text{ and } \frac{\partial}{\partial tx}\frac{\partial Wx}{\partial Wo} = \frac{-1}{to + ts}$$

That is, higher *tx* imply more *o* is consumed.

Notice that if *x* were an exotic prey item it would be expected to have high *tx* and would be skipped, as with *O. cuniculus* in Chile (see Fig. 4b). The value of *tx* is a coevolutionary result of the predator-prey interaction, where the former tend to decrease *tx* whereas the opposite is true for the prey.

The *L. monticola-Camponotus* situation is different. The chemistry of ants and non-ant insects is probably different (see above) and the consumption frontier would therefore be concave (Fig. 4c). Indifference curves on the other hand would have relatively low values of *tx*, since ants are relatively small, slow, do not fly or jump, and consequently have low pursuing plus handling time. Hence, if the lizard has the appropriate detoxicating machinery, the optimal diet is likely to be monophagy towards ants (see Fig. 4c).

ACKNOWLEDGMENTS

Johanna Filp made useful suggestions on the manuscript. Research reported in this contribution has been generously supported by Universidad Católica de Chile through grant DIUC 113&— TO Eduardo R. Fuentes.

RESUMEN

En esta contribución se documenta la adaptación de dos clases de vertebrados predadores a sus presas, y luego se muestra la relación entre los dos tipos de respuesta por medio de un modelo económico.

El primer caso expuesto corresponde a la relación entre el conejo *(Oryctolagus cuniculus)* y sus supuestos predadores en la zona central de Chile. *O. cuniculus* fue recientemente introducido en Chile, y su actividad en los alrededores de Santiago difiere marcadamente de la que desarrolla en sus zonas de origen (Mediterráneo occidental). En Europa, *O. cuniculus* vive estrechamente asociado a los arbustos (al igual que los conejos nativos del chaparral californiano), lo cual se ha interpretado como una adaptación conductual asociada a la reducción de la presión de predación. Sin embargo, en la zona central de Chile, *O. cuniculus* desarrolla su actividad en las zonas expuestas entre los arbustos (al igual que los conejos californianos que habitan en islas).

La actividad de los conejos en el terreno puede estimarse por el patrón de distribución de sus fecas con respecto a los arbustos. En el caso de *O. cuniculus* en la zona central de Chile, sus fecas son depositadas en gran número en las áreas entre los arbustos, y en escasa cantidad bajo los arbustos (véase Fig. 1). Este patrón de deposición de fecas contrasta con el que presentan los conejos nativos californianos, que hacen precisamente lo contrario (véase Fig. 2).

Por otra parte, la distribución de fecas de los conejos californianos es muy similar a la que presenta el roedor nativo chileno *Octodon degus* (véase Fig. 2), y en ambos casos se ha postulado que esta restricción de actividad resulta de la presión que ejercen los predadores. Esta explicación se ve avalada por el conocimiento de una gran cantidad de predadores que efectivamente se alimentan de las especies mencionadas (véase tabla I y texto).

En cambio, aun cuando en Chile existen predadores potenciales para los conejos, *O. cuniculus* se comporta como si no existieran predadores, o éstos fueran inefectivos. Este último parece ser el caso, dados los antecedentes de la literatura y las colectas de fecas y egagrópilas de predadores realizadas por los autores (véase tabla I y texto).

En conclusión, los conejos nativos *(O. cuniculus* en Europa, conejos californianos) exhiben restricción de su actividad en el hábitat en presencia de predadores efectivos, pero extienden su actividad a zonas expuestas cuando se ven libres de ellos (conejos en islas), o cuando los predadores son inefectivos (zona central de Chile). En este caso se puede decir que los predadores nativos chilenos no incluyen al conejo introducido como presa.

El segundo caso que se documenta en este trabajo es el opuesto del anterior. Aquí la situación se refiere a la estricta especialización del lagarto *Liolaemus monticola* (Iguanidae) en el consumo de hormigas de un solo género (*Camponotus),* en contraste con los hábitos de otros lagartos del mismo género que son mucho más católicos en sus dietas .

Los autores suponen que esta diferencia en hábitos predadores estaría relacionada con la capacidad diferencial de detoxificación de las presas ingeridas que presentaría *L. monticola* con respecto a otros *Liolaemus.* Al hacer esta proposición, los autores hipotetizan que los insectos que componen las dietas de estos lagartos posiblemente conforman un mosaico complejo de toxinas que requieren ser detoxificadas para su asimilación o excreción. Este fenómeno ya ha sido documentado extensamente en insectos fitófagos, pero hasta ahora no había sido considerado como posible factor operante en la selección o especialización de predadores vertebrados por sus presas.

Es sabido que en vertebrados el hígado es un órgano importante en la detoxificación de toxinas, y que se ve hipertrofiado cuando éstas son incorporadas en exceso a la dieta. Con estos antecedentes se podría esperar sustento a la hipótesis de toxicidad de la dieta de insectos, si es que *L. monticola* (monófago) tuviera el hígado más liviano que otros *Liolaemus* de dieta menos especializada.

Efectivamente, éste es el resultado que se obtiene al comparar el peso seco del hígado (ponderado por el peso seco corporal) de ocho especies de *Liolaemus* chilenos, con respecto a la diversidad trófica de sus dietas (véase Fig. 3). Este hecho sustenta la hipótesis de toxicidad de las dietas propuesta por los autores, y además

sugiere que la especialización de un predador en determinada presa puede ser no sólo conductual sino también fisiológica, relacionada con la composición química de ella.

Los dos casos analizados pueden ser interpretados mediante un modelo económico (véase Fig. 4), en que se relacionan las propiedades químicas (toxicidad) y físicas (facilidad de captura) de las presas, con el beneficio que obtiene el predador al incorporar (o desechar) un nuevo ítem de presa en su dieta (caso predadores nativos-conejos introducidos), o al especializarse en un solo ítem (caso *L. monticola-Camponotus).*

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