Comparación de Métodos para
Calcular el Area de Actividad
de *Sceloporus scalaris*

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y
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COMPARACION DE METODOS
PARA CALCULAR EL AREA DE ACTIVIDAD
DE *Sceloporus scalaris*

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RESUMEN

Los datos de recaptura de la lagartija *Sceloporus scalaris,* de la Reserva de la Biosfera de La Michilía en el Estado de Durango, México, fueron anali- zados utilizando 7 estimaciones diferentes del área de actividad, 3 de las cuales son poli- gonales y las otras 4 estadísticas. Los métodos poligonales se muestran en general sensi- bles al tamaño de la muestra y los estadísticos no, pero éstos tienden a sobreestimar el área utilizada. Los machos tienen un área mayor que la de las hembras independiente- mente del método utilizado. Contrastando los resultados obtenidos con el rastreo conti- nuo de los individuos en el campo, se encontró que el método del polígono mínimo es el que evalúa de manera más realista el área más utilizada por los individuos de esta especie y que el modelo bivariado por componentes del 68% es el más adecuado para estimar el área recorrida por los mismos en sus desplazamientos.

ABSTRACT

Recapture data for the Lizard *Sceloporus scalaris* (Sauria: Iguanidae) from the Michilía Biosphere Reserve in the State of Durango, México, were analyzed by 7 different home range methods: three of them polygonal and the other four statistical. Polygonal methods are sample size biased; statistical methods are not sample size biased, but tend to overestimate the used area. Males had larger home ranges than females regardless of method. Home range estimates were compared with the actual home ranges obtained from continuous observations and tracking of lizards in the field. The minimum polygonon method most realistically approximates the area most frequently used by individuals in this population, while the bivariant model of 68% is the best estimator of the area used by lizards in their actual movements.

INTRODUCCION

El área de actividad también conocida como dominio vital, ámbito hogareño o "home range", es el área que un animal ocupa durante sus actividades normales de alimentación, apareamiento y cuidado de crías (Burt, 1943). El área de actividad es un importante atributo adaptativo de los individuos, directamente relacionado con parámetros y características de los mismos, tales como su vigor y agresividad, la eficiencia de su movimiento y sus necesidades metabólicas (Milstead, 1972; Schoener, 1971; Simon, 1975; Turner *et al.,* 1969), también está relacionado con atributos de la población a la que pertenecen los organismos, como la densidad, la competencia intraespecífica y la organización social (Brown, 1969, 1975; Krebs, 1971; Schoener, 1968), y a características de la comunidad a la que pertenece la población, tales como las relaciones interespecíficas y la utilización diferencial de los recursos (Orians y Wilson, 1964).

A pesar de que el concepto de área de actividad es claro, el principal problema para trabajar con este atributo es el de cuantificarlo. En la actualidad existen no menos de 17 formas diferentes de evaluarlo. (Aguirre *et al* 1984; Fitch, 1958; Hall, 1971; Harvey y Barbour, 1965; Hayne, 1949; Jenrich y Turner, 1969; Koepl *et al,* 1975; Metzgar y Scheldon 1974; Milstead, 1971; Mohr, 1947; Mohr y Stumpf, 1966; Rose y Judd, 1975; Schoener, 1981; Southwood, 1966; Stumpf y Mohr, 1962; Van Winkle *et al,* 1973).

Existen trabajos previos interesantes en los que se comparan resultados al utilizar los diferentes métodos; sin embargo, en algunos de estos trabajos se comparan los resultados obtenidos con diferentes métodos, pero con datos provenientes de fuentes también distintas (Rose, 1982), o se comparan los mismos datos pero con solo de 2 a 5 métodos diferentes (Ernst, 1970; Jorgensen y Tanner, 1963; Waldschmidt, 1979). En el presente estudio se comparan los resultados para el área de actividad de *Sceloporus scalaris* (Sauria: Iguanidae), obtenidos a través de los 7 métodos más utilizados en la literatura, y para lo cual se varió exclusivamente el método elegido para estimarla, manteniendo constantes todos los otros factores extrínsecos, e intrínsecos que pueden modificarla.

Materiales y Métodos

El presente estudio se llevó a cabo en la Reserva de la Biosfera de La Michilía*, en el Estado de Durango, México (23°20' - 23°30' N; 104°07' - 104°20' W). La elevación del área es de aproximadamente 2480 m, la temperatura media anual varía entre 17.4°C y 20.4°C y su precipitación anual entre 525 y 609 mm, estando prácticamente concentrada en el verano (junio a septiembre). Aunque la vegetación de la zona está muy diversificada, pudiéndose distinguir 11 unidades diferentes (Martínez y Saldívar, 1978), la comunidad vegetal más importante es el bosque de encino-pino. En una zona abierta de tal bosque, localizada a 5 km al norte de la estación de campo del Instituto de Ecología en la Reserva, se marcó un rectángulo de 50 x 200 m por medio de estacas separadas una de otra por 10 m, cada estaca tenía un número distintivo. Dentro de este rectángulo fueron capturados a mano y marcados por el doble método de pequeñas manchas de pintura (temporal) y corte de dedos (permanente) 78 individuos adultos de *S. scalaris* en mayo de 1981, una vez marcados se procedió a recorrer sistemáticamente este transecto durante 21 días en ese mismo mes de 4 a 6 hrs. diariamente e iniciando cada vez desde un punto diferente del mismo, de tal forma en que todas sus secciones fueron recorridas a todas las horas posibles. De cada individuo sobre el que se efectuaba una recaptura se anotaba (entre otros datos) el de su localización exacta, tomada como una medida bicordenada a la estaca más cercana. Es necesario mencionar que debido a que las recapturas son visuales y a que sólo se toma el primer punto observado cada día para cada inviduo, la técnica no altera de forma tal la conducta de los individuos como para sesgar los resultados; por otro lado, la heterogeneidad del habitat tampoco modifica la efectividad de la técnica, dado que el 89.1% de los desplazamientos de los individuos de esta especie ocurren sobre el suelo (Ortega *et al.* 1982), es decir en un microhabitat bidimensional.

Los datos de aquellos individuos con menos de 3 puntos de localización y de aquellos cuya área de actividad quedara en las zonas limítrofes del transecto se desecharon, trabajándose solamente con los puntos de recaptura de 42 individuos que fueron pasados a ma-

* La Reserva de la Biosfera de La Michilía es parte del programa El Hombre y la Biosfera (MAB) de la UNESCO.

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pas a escala de la zona y en un sistema bicoordenado en papel milimétri-
co, determinándose su área de actividad por los siguientes métodos poli-
gonales y estadísticos; poligonales: polígono convexo (Southwood,
1966) polígono mínimo (Mohr 1947; Stickel, 1954), polígono mínimo mo-
dificado (Harvey y Barbour, 1965); estadísticos: función denso-probabi-
lística o de radio-recaptura (Hayne, 1949; Dice y Clark, 1953; Calhoun y
Casby, 1958), función elíptica de covarianza (Jenrich y Turner, 1969),
modelo bivariado por componentes (Koepl *et al,* 1975) y el bivariado por
componentes del 68% (Aguirre *et al,* 1984).

RESULTADOS

Las propiedades de cada método utilizado se
reflejan en los resultados obtenidos en metros cuadrados para el área de
actividad por cada uno de ellos (Cuadro No. 1), observándose que dentro
de los métodos poligonales con el que encontramos un área mayor, en
casi todos los casos, es con el del polígono convexo, un área más peque-
ña con el mínimo y una aún más reducida con el modificado. Dentro de los
métodos probabilísticos en general el área estimada por la función den-
so-probabilística es mayor que la de la función elíptica de covarianza y
que la del modelo bivariado por componentes del 68%, pero menor que la
del bivariado por componentes del 95%.

En el siguiente Cuadro (No. 2) es posible obser-
var claramente una de las principales desventajas de los métodos poligo-
nales, que es la de que éstos son radicalmente sensibles al tamaño de la
muestra, es decir, a mayor número de recapturas, en cada ocasión es
mayor el tamaño del área estimada, y así, para poder hacer comparativos
los resultados obtenidos por uno de estos métodos, necesitamos trabajar
con gran cantidad (y la misma) de recapturas y en cortos períodos de
tiempo, y aunque existen métodos para corregir esta desviación (Jenrich
y Turner, 1969) éstos tienen también inconvenientes (Rose, 1982).

Como se puede apreciar en el mismo Cuadro
No. 2, los métodos probabilísticos no son sensibles al tamaño de la mues-
tra; sin embargo, adolecen también de sus defectos, siendo el principal el
de sobreestimar el área utilizada por los individuos, ya que asignan la pro-
babilidad de encontrar un animal donde nunca fue observado. Además,

Cuadro 1.

Areas de actividad (m^2) para algunos de los individuos de *Sceloporus scalaris,* estudiados por los diferentes métodos utilizados.

Individuo sexo y número	METODOS POLIGONALES			METODOS PROBABILISTICOS			
	Polígono convexo	Polígono mínimo	Polígono modificado	Fun. denso-probabilíst.	Elíptico matriz cov.	Bivariado por componentes 95%	68%
♀ 182	85.6	8.0	8.0	799.92	682.72	1,841.75	226.19
♀ 132	251.2	201.6	44.0	5,076.17	2,352.0	11,083.53	1,954.18
♂ 13	24.0	16.4	16.4	125.92	146.05	1,174.95	329.86
♂ 14	512.8	252.0	188.8	1335.95	1,243.84	1,664.79	627.31
♂ 15	486.8	298.4	93.3	1,409.51	1,124.86	1,484.40	508.68
♂ 135	245.6	230.4	230.4	3,292.70	3,058.70	6,745.22	1,402.69
♂ 71	237.2	222.4	224.4	2,511.70	226.61	5,780.53	804.66
♂ 109	460.0	436.0	436.0	2,763.61	3,029.47	8,815.31	1,847.49
♂ 151	262.4	258.0	82.4	1,639.92	2,082.27	439.82	374.63
♂ 191	32.8	32.8	32.8	327.98	223.79	1,119.97	162.57
♀ 84	18.0	18.0	18.0	207.85	118.65	747.69	785.59
♀ 26	56.0	56.0	56.0	661.82	892.43	2,012.19	402.91
♂ 141	212.8	212.8	212.8	2,144.06	2,772.72	18,284.06	2,042.03
♂ 113	56.8	56.8	56.8	844.76	920.26	5,428.70	603.19
♂ 209	72.8	72.8	72.8	1,875.60	5,502.23	4,853.76	565.48
♀ 81	9.6	9.6	9.6	168.61	227.88	19,339.64	365.21
♀ 85	24.8	24.8	24.8	995.89	413.55	28,550.79	1,968.88
♀ 59	54.0	54.0	54.0	1,099.55	1,012.10	80,223.70	424.11
♀ 83	6.8	6.8	6.8	172.79	152.36	1,149.82	53.41
♀ 184	28.0	28.0	28.0	662.44	609.44	9,299.11	285.36
♂ 168	59.6	59.6	59.6	3,879.87	1,284.17	587,634.89	2,733.18

Cuadro 2.

Promedio de actividad (m^2) de *Sceloporus scalaris,* separada en grupos por número de recapturas y sexo (entre paréntesis aparece el número de individuos).

Número de Recapturas	METODOS POLIGONALES			METODOS PROBABILISTICOS			
	Polígono convexo	Polígono mínimo	Polígono modificado	Fun. denso-probabilíst.	Elíptico matriz cov.	Bivariado por componentes 95%	68%
3							
♀ (10)	26.7	26.7	26.7	584.22	525.11	34,640.76	609.57
♂ (7)	35.8	35.8	35.8	1,976.61	738.22	587,634.89	1,425.88
4							
♀ (5)	35.3	35.3	35.3	548.44	438.82	1,379.94	509.19
♂ (6)	100.5	100.5	100.5	1,964.29	3,352.73	9,522.17	1,070.23
5 ó más							
♀ (4)	168.4	104.4	26.0	2,936.05	1,517.36	6,462.64	1,090.18
♂ (10)	261.3	201.3	146.7	1,675.91	1,477.28	1,127.97	757.23

por ejemplo, el método de la función denso-probabilística asume que existe una distribución uniforme de los puntos de localización de los individuos, es decir, se basa en el planteamiento de que existe la misma probabilidad de desplazamiento en cualquier dirección, lo cual no se cumple cuando existen presiones sociales territoriales o habitats no homogéneos, es decir, no funciona casi siempre.

El tamaño del área de actividad para las hembras es siempre menor, independientemente del método utilizado, que para los machos (Cuadro No. 3), siendo en este caso 11.9 veces mayor para estos últimos en promedio general.

DISCUSION

En este atrabajo se pone de manifiesto la dicotomía reiteradamente planteada por autores previos en relación con las características de los métodos poligonales y estadísticos, pues ambos tienen ventajas y desventajas que son principalmente las que han sido mencionadas un poco arriba, además de que con los métodos poligonales con los mismos datos, diferentes autores pueden obtener distintos resultados, lo cual es una obvia desventaja; pero también los métodos estadísticos pueden sufrir serias desviaciones si los datos no se apegan a la distribución supuesta y si no toda el área que engloba ésta, es adecuada para el organismo de tal forma en que éste no se pueda mover libremente y al azar dentro de ella. Los modelos estadísticos además son incapaces para establecer límites entre áreas de actividad contiguas. Sin embargo, la polémica continúa (Rose, 1982; Waldschmidt, 1979) y así existen autores que defienden y prefieren la utilización de los métodos poligonales (Milstead, 1972) mientras otros los estadísticos (Jorgenssen y Tanner, 1963; Tinkle, 1967).

En nuestro caso, al contrastar los resultados obtenidos con los diferentes métodos con aquellos que se obtuvieron al rastrear sin interferir (desde lejos y con binoculares) en el campo a varios individuos de esta especie por varios días consecutivos, encontramos que el método más apropiado para evaluar el área más utilizada por los organismos —asociada inclusive a las perchas de asoleo y sitios de refugio— es el del polígono mínimo y que el método que evalúa de manera más repre-

Cuadro 3.

Promedio de áreas de actividad (m^2) para los dos sexos de *Sceloporus scalaris* por los diferentes métodos utilizados.

METODOS POLIGONALES

	Polígono convexo	Polígono mínimo	Polígono modificado
♀	76.81	29.34	29.34
♂	144.51	112.55	94.35

METODOS PROBABILISTICOS

	Fun. denso-probabilíst.	Elíptico matriz cov.	Bivariado por componentes 95%	68%
♀	1,356.23	827.09	14,161.13	736.31
♂	1,872.27	1,856.07	199,428.34	1,084.44

sentativa los desplazamientos en el área recorrida por los mismos es el del modelo bivariado por componentes del 68%.

El método bivariado por componentes del 68%, es una modificación al bivariado de Koepl *et al.* (1975). El principal inconveniente de este último es el de trabajar de forma arbitraria con dos desviaciones estándar, lo cual introduce un serio error de cálculo al incluir puntos localizados en la periferia, que representan zonas de utilización accidental o escasa, y que no forman parte consistente del ámbito hogareño, la modificación planteada por Aguirre *et al.* (1984) de trabajar con una sola desviación estándar, contribuye sustancialmente a reducir esta sobreestimación.

Para los individuos adultos de *Sceloporus scalaris* en esta zona y en esta época del año, son indudablemente este método poligonal y este estadístico los dos métodos que evalúan de una manera más realista el área de actividad.

AGRADECIMIENTOS

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MANDIBULAR FORCE OF ADULT AND LARVAL
PASSALIDAE IN FAMILY GROUPS*

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RESUMEN

La fuerza de las mandíbulas de larvas y adultos de grupos familiares de diversas especies de coleópteros de la familia Passalidae fue medida mediante un dinamómetro. Los resultados muestran diferencias significativas entre las fuerzas ejercidas por los adultos y las larvas, situándose los adultos tenerales entre estos dos extremos. En vista de la disparidad de las fuerzas mandibulares entre adultos y larvas, estas últimas dependen para su alimentación de los pedazos de madera que los adultos extraen de las paredes de las galerías donde habitan. Es evidente que el comportamiento subsocial presentado por este grupo de insectos, está reforzado por esta dependencia alimentaria de la larva.

ABSTRACT

The mandibular force of larvae and adults of family groups of various species of Coleoptera of the family Passalidae was measured with a dynamometer. The results show significant differences between the mandibular forces of adults

and of larvae, while teneral adults showed intermediate strengths. The differences in mandibular force indicate that the feeding of the larvae depends on the pieces of wood that the adults extract from the walls of their galleries. The food dependency of the larvae reinforces the subsocial behavior of this group.

INTRODUCTION

Passalid beetles are known to be subsocial. The only known life cycle within this group is that of the Northamerican species *Odontotaenius disjunctus* (Illiger), described by Gray (1946). Partial data gathered to date on the life cycle of some tropical species show similarity in all major respects with *Odontotaenius.* The extent to which subsociality is obligatory has been the subject of debate in the past. Four recent studies coincide in considering passalid beetles to possess one of the highest levels of subsocial behaviour known for insects (Schuster and Schuster 1985; Reyes-Castillo and Halffter 1983, 1984; Valenzuela-González and Castillo 1983).

One area of discussion has centred on the feeding of the larvae by the adults of a family group. The adults chew wood from the ends of the family's living-galleries into splinters and the larvae in turn chew the splinters. Ohaus (1900) suggests that this behavior occurs because the mandibles of the larvae are too weak to remove splinters directly from the walls of the galleries, while Heymons (1929) and Pearse *et al.* (1936) have denied this. In the present work, larvae and adults have been caused to nip a dynamometer with their mandibles and the maximum forces registered in such nips have been measured with a view to quantifying one of the capabilities which the animals must use if they are to remove splinters from gallery walls.

MATERIALS AND METHODS

The experimental protocol and the apparatus used in these experiments were in the main identical with those described previously (Jarman 1980); the only change made was that a third dynamometer lever, even smaller than the two previously described, was available. This third lever was small enough to be placed between mandibles

only 0.5 mm apart and it had a compliance of 1.1 μm per gram-weigh (113 μm per Newton).

Animals were only used for these experiments when adults and larvae were found together in the same tunnel. Such suitable families were found while collecting during August and September 1982 in different localities of the States of Puebla and Chiapas, México (Table 1).

Each individual was caused to squeeze the dynamometer lever ten times while being stimulated by the experimenter in such ways as seemed to result in the most forceful nips on the lever by the mandibles. This was normally a combination of handling and breathing on the insect.

RESULTS

Table 1 shows the results obtained from those family groups where at least two larvae and a mature black adult were collected, appeared in good condition and lived for at least a week after the experiments (normally they survived for much longer). In no case did omitted data contradict the published results.

In every family group studied, the mandibles of the larvae all squeezed the apparatus much less strongly than did those of the weakest adults, as shown in Table 1. Ranking the forces in increasing order within family groups, letting L and A represent forces produced by larva and adult respectively, we have for group 2 LLLAA, for family 5 LLLLA and for group 9 LLAA. The probability of an arrangement as extreme as this occurring by statistical fluctuations if the adults were not consistently stronger that than the larvae would be only 0.001. If we disregard the information inherent in the pairing of adults with larvae *of the same species, of the same family group,* and instead just treat the fourteen insects as a single group of medium-sized passalids, the series is LLLLLLLLLAAAAA, whit a probability of only 4×10^{-6}.

To put the large difference between larvae and adults into perspective, a larger database than that presented here is needed. This is made up by accreting to the data that are presented above the previously-published data of Reyes-Castillo and Jarman (1981) as well as some unpublished data that have accumulated since then. The augmen-

Table 1.

List of passalid specimens used in this work. Each individual nipped the dynamometer ten times. The figure in the last column is the force in grams - weight exerted in the greatest nip, while that in previous column is the mean of the forces of the ten nips.

SPECIES	SEX/ STADIUM	MASS (g)	Force (g-wt)	
			MEAN	GREATEST
Family 2	Larva III	0.35	4.70	8.64
Heliscus	Larva III	0.35	4.55	11.2
tropicus	Larva III	0.40	5.92	9.63
(Percheron) [a]	♀ Adult	0.53	114.9	146.1
	♂ Adult	0.49	106.2	120.8
Family 5	Larva III	0.31	28.1	38.9
Passalus (Pertinax)	Larva III	0.33	26.8	46.4
punctatostriatus	Larva III	0.37	35.4	48.7
(Percheron) [a]	Larva II	0.26	16.2	32.6
	Adult teneral	0.32	16.6	27.2
	♂ Adult	0.41	135.0	170.9
Family 9	Larva III	0.69	7.26	18.2
Odontotaenius	Larva III	0.76	6.59	10.6
striatopunctatus	♀ Adult	0.83	183.2	221.2
(Percheron) [a]	♂ Adult	0.74	164.2	180.5
Family 8				
Heliscus	♀ Adult	0.47	136.1	158.3
vazquezae [a]	♂ Adult	0.61	169.1	230.6
Reyes-Castillo y Castillo	♀ Adult	1.21	252.5	342.5
	♂ Adult teneral	0.74	89.1	119.5
	♀ Adult teneral	0.69	76.3	90.2
Family				
H. vazquezae [c]	♀ Adult	1.02	200.4	288.4
	♂ Adult	0.89	134.1	169.9
Family 10				
Proculejus	♀ Adult	1.40	138.7	208.5
brevis (Truqui) [b]	♂ Adult	1.32	79.2	139.0

SPECIES	SEX / STADIUM	MASS(g)	Force (g-wt)	
			MEAN	GREATEST
Family *P. brevis* **b**	♀ Adult	2.08	151.5	262.3
	♀ Adult	1.36	141.4	205.1
	♂ Adult	1.47	271.4	352.5
	♂ Adult	1.67	176.8	288.4
Family 1 *Heliscus tropicus* (Percheron) **a**	♀ Adult	0.68	134.4	196.5
	♀ Adult	0.71	170.0	208.1
	♂ Adult	0.68	127.1	219.0
	Larva III	0.43	8.72	13.9
Family *Proculus beckeri* (Zang) **d**	♀ Adult	6.48	750.3	897.4
	♂ Adult	7.26	759.9	1015.0
	♂ Adult	7.26	457.8	668.7
	♂ Adult	6.70	571.0	715.8
Family Unidentified	Adult	0.24	86.9	99.5
	Larva	0.20	5.79	7.69
	Larva	0.20	6.24	13.2
Miscellaneus specimens *Oileus heros* (Truqui) **c** *Petrejoides orizabae* Kuw. **c** *H. vazquezae* **c**	Adult	4.10	282.1	355.1
	Adult	0.28	58.1	88.3
	♀ Adult	1.09	241.0	262.8
	♂ Adult	0.88	211.2	237.6
Unidentified	Adult	0.28	167.7	209.7
	Adult	0.28	188.8	218.6

g - grams, g-wt grams/weight.
Números romanos: second (II) and third (III) larval instars.
a - Barranca de Patla, Puebla.
b - Camotepec, Piedras Encimadas, Puebla.
c - Xicotepec de Juárez, Puebla.
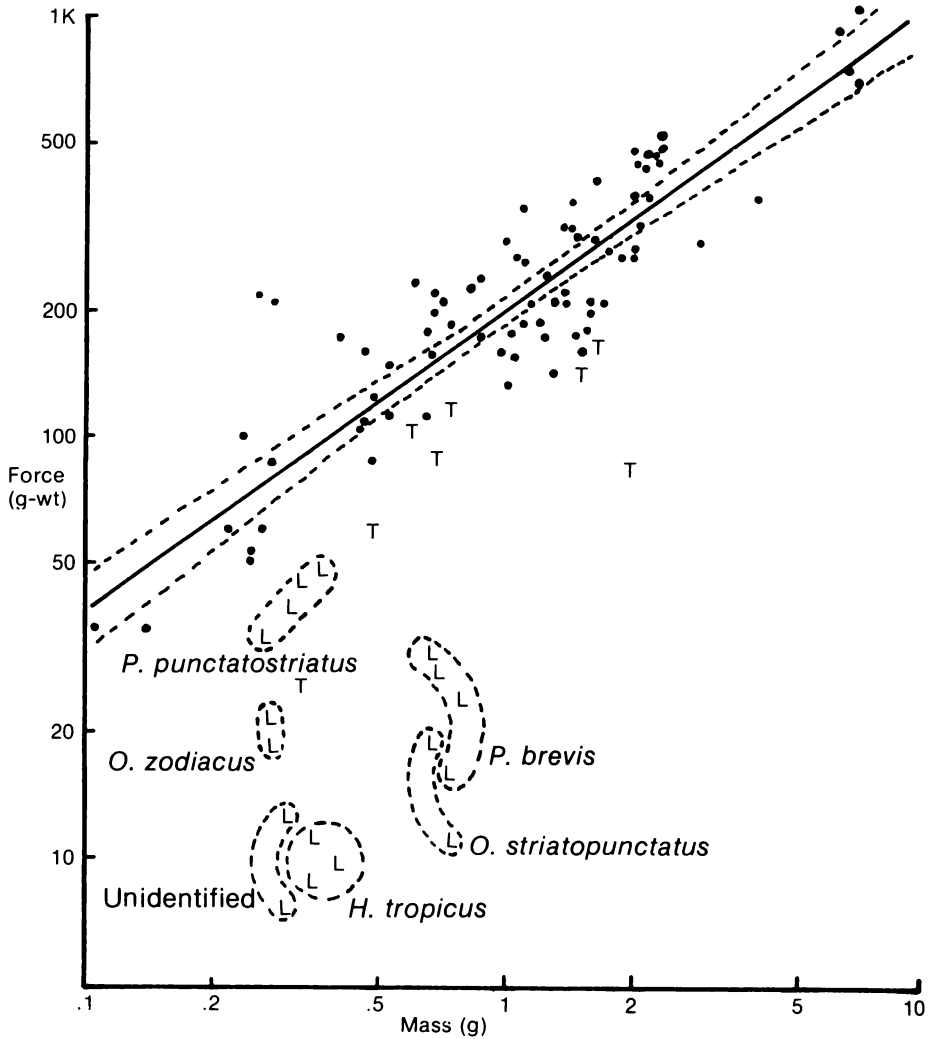**d** - El Bosque, La Trinidad, Chiapas.

Figure 1.
            Graph connecting maximum force exerted by the mandibles of passalids with their mass. The broken lines indicate 95% probability limits for predictions of the force that might be exerted by the typical adult of a given mass. Also shown are points plotted for larvae (L) and teneral adults (T) that have been measured. Both scales are logarithimic.

ted database, which is presented graphically in Fig. 1, rests on species of widely divergent sizes, and so the sizes of the individual specimens have to be taken into account; it is no longer reasonable to classify the entire experimental group as "medium-sized passalids". The line plotted is the regression line of log (mandibular force) on long (mass). The force of the strongest of ten measured nips was used for this. Also plotted as broken lines are the 95% confidence limits for the regression. The residual deviations of the points from the regression line show approximate normality on the moments test (e.g. Fisher, 1946). The regression line was found to be represented by the relation:

$$\text{long (force)} = 2.286 + 0.702 \text{ long (mass)}$$

or equivalently:

$$\text{force} = 193 \text{ (mass)}^{0.702}$$

where force is measured in grams-weight, mass in grams and logarithms are to base 10. The standard error of the slope is $\pm$ .043

While the deduced relationship between mandibular force and mass for adults is reasonable and free from anomalies, the same cannot be said for the corresponding relationship among the larvae tested, and the best that can be done is to treat the family groups of larvae individually. After averaging logarithms of mass and force within each family group, the third stage larvae of *Odontotaenius striatopunctatus* turn out to exter 11.1 times less mandibular force than does a hypothetical passalid adult of the same mass as the larvae. Third stage *Heliscus tropicus* larvae are 9.8 times less strong than adults of the same mass and those of an (as yet) unidentified species 6.2 times less strong. Data form Reyes-Castillo and Jarman (1981) show third stage *Proculejus brevis* larvae nipping 6.6 times less strongly and second stage *Odontotaenius zodiacus* 3.8 times. Out of line with these results is a family of four second and third stage larvae of *Passalus (Pertinax) punctatostriatus,* which nipped only 2.1 times less strongly than did adults of like mass. For purposes of comparison, a convenient rule-of thumb for these species is that an adult has about 1 ½ times the mass of the third-stage larva of the same species.

Three adventitious results of this research have been the findings that (i) no significant difference was found between the mandibular strengths of male and female adults of the same family group,

(ii) the strengths of teneral adults usually fell between those of larvae and those of mature black adults and (iii) the strengths of the Passalid larvae fell far short of those of a 2-gram Scarabaeid larva (326 g-wt) and two larvae of the Dynastinae *Strategus aloeus*(Lin.) of masses 12 and 17 grams and mandibular forces 516 and 686 g-wt respectively that were also tested. This Scarabeid larvae are solitary and live in galleries dug in rotting wood, under very similar conditions to passalid beetles.

CONCLUSIONS

Given such a great disparity between the measured mandibular forces of larva and adult, we are forced to conclude that either the adult mandibles are far too strong for gnawing wood (in which case we must postulate and additional function for such strong appendages) or else that the larval mandibles are much too weak for gnawing wood. The more reasonable of these possible conclusions is that the larvae are mechanically incapable of breaking off splinters of wood from the concave interior surfaces of their living-tunnels and that this is linked with the subsocial habit of Passalidae. Many authors have commented on the fact that larvae feed on wood particles that been off by the adults and Gray (1946) notes the fineness of these particles in comparison with the coarseness of chips that are formed when adults first start a tunnel and no larvae are present.

It must be remembered, too, that strong (and properly shaped) mandibles are not the only requirement for efficiently breaking off chips of wood from the concave interior surface of the tunnel. The gnawing may be described as a three-stage process: (1) the open mandibles must be pushed into the surface of the wood, (2) the mandibles must grip wood between them by their closing force and (3) the gripped chip must be either scissored off by the same closing force or else pulled out by a pulling force exerted partly by the legs and aided, perhaps, by head-waggling, etc. The present work concerns itself only with the force involved in the second of these three stages; its conclusions are reinforced by the notion that larvae are not equipped to provide the pushing force for the first stage. Even if they were, the larvae would find it hard to engineer a point d'appui that prevented their bodies slipping while they were attempting to drive their open mandibles into the wood surface.

Thus the balance of evidence is that larval Passalidae of the species studied could not feed themselves by chewing wood splinters directly from the walls of the tunnels in which they live because their mandibles do not grip with enough force to do this, as well as for other reasons. Subsocial behaviour therefore seems to be obligatory, not facultative, for the larvae at their present stage of evolution. We know little of the evolutionary events that led to either subsocial behaviour or the weakness of the larval mandibles and cannot therefore say that either 'caused' the other nor wherther both were independently caused by a third evolutionary pressure.

ACKNOWLEDGEMENTS

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ERRORS OF MEASUREMENT OF
MAXIMUM POSSIBLE PERFORMANCE

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In a previous paper, the author attempted to measure the maximum possible force which individual passalid beetles could exert between their mandibles. This was done by the rough-and-ready method of encouraging each individual beetle to nip ten times on a dynamometer and counting the strongest of the ten nips as representative of the greatest force that the beetle could ever possibly exert in the circumstances; this latter will be called the 'ultimate performance' in this paper. Clearly this measurement, the greatest performance of the ten trials, falls somewhat short of the ultimate performance, and in this paper attempts are made to estimate that shortfall.

The first step in the estimation was to assume that the forces of the ten measured nips of a particular individual were independent samples drawn from some probability-distribution of nip-forces of the general nature of that depicted in Fig. 1; the essential feature of this is that there is a definite force, arrowed in Fig. 1, above which the probability of observing that force is zero. The curve may approach the force axis at an angle or tangentially at that point. The distribution is to be estimated for each individual beetle and the force corresponding to the arrowed point used as the estimate of the ultimate force.

Secondly the assumption is made that, although this force-distribution curve will shift along the force axis according to whether it is to apply to a strong or a weak beetle, and although it will be broad or narrow according as to whether it is to apply to a variable or a consistent individual, nevertheless the form of the curve (i.e. the specification of whether the curve is rectangular, sawtooth-shaped, parabolic, of cosine-form etc.) will be similar for all individuals.

Thirdly, the form of the curve was estimated. To do this, the same individual (selected as appearing to be in good condition
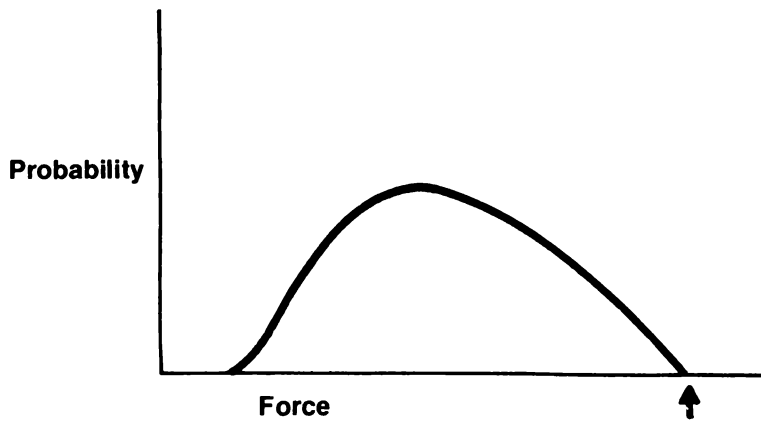
Fig. 1. Suggested general form for the probability distribution of forces measured in a beetle. The 'ultimate performance' is indicated by the arrow.

Table 1 An arbitrary library of distribution functions useful in estimating ultimate performance.

	Shape	Probability distribution function	Mean	Standard deviation	Cumulative distribution function	Shortfall	Coefficient of variability
a		$p = \dfrac{1}{a}$ $0 < x < a$	.50a	.29a	$\dfrac{x}{a}$	.091a	.91
b		$p = \dfrac{2x}{a^2}$ $0 < x < a$	.67a	.24a	$\dfrac{x^2}{a^2}$	.048a	.95
c		$p = \dfrac{2}{a}\left(1 - \dfrac{x}{a}\right)$ $0 < x < a$	.33a	.24a	$\dfrac{x}{a}\left(2 - \dfrac{x}{a}\right)$	.27a	.49
d		$p = \dfrac{x}{a^2}$ $0 < x < a$ $p = \dfrac{1}{a^2}(2a - x)$ $a < x < 2a$	a	.41a	$\dfrac{x^2}{2a^2}$ $0 < x < a$ $\dfrac{1}{2}\left(-2 + \dfrac{4x}{a} - \dfrac{x^2}{a^2}\right)$ $a < x < 2a$	.38a	.49
e		$p = \dfrac{1}{2}\sin x$ $0 < x < \pi$	1.57	.68	$\dfrac{1}{2}(1 - \cos x)$	.55	.51
f		$p = \dfrac{3}{4a^3}(a^2 - x^2)$ $-a < x < a$	0	.45a	$\dfrac{1}{4}\left(2 - \dfrac{x}{a}\right)\left(1 + \dfrac{x}{a}\right)^2$	.34a	.53
g		$p = \cos x$ $0 < x < \pi/2$	.57	.38	$\sin x$	.39	.50
h		$p = (2+\sqrt{2})\sin\left(x + \dfrac{3\pi}{4}\right)$ $0 < x < \pi/4$	.27	.19	$(1+\sqrt{2})(\cos x + \sin x - 1)$	.21	.50
j		$p = \dfrac{2}{\pi}\sin^2 x$ $0 < x < \pi$	1.57	.57	$\dfrac{1}{\pi}\left(x - \dfrac{1}{2}\sin 2x\right)$	.71	.37
k		$p = \dfrac{4}{\pi}\cos^2 x$ $0 < x < \pi/2$	.47	.32	$\dfrac{1}{\pi}(2x + \sin 2x)$	.56	.36
l		$p = \dfrac{4}{(\pi-2)}(1 - \sin 2x)$ $0 < x < \pi/4$	.20	.15	$\dfrac{2}{(\pi-2)}(2x + \cos 2x - 1)$	.31	.35

and not 'tiring' easily) had the forces of 100 nips measured instead of the customary 10. From the arbitrary library of curves listed in Table 1, the one was selected which showed the best fit between the cumulative frequency distributions of the curve and of the 100 observations. Goodness of fit was measured by the Kolmogorov-Smirnov statistic or a sum-of-squares statistic (both gave the same answer in this case). A power transform was applied to the measured forces to yield a distribution with zero skewness whenever comparison was being made with a theoretical curve that was symmetrical. Once skewness had been dealt with, the standard deviation of the experimental distribution was matched to that of the theoretical, either by scaling the forces (curves e, g, h, j, k & l of Table 1) or by selecting appropriately the width parameter a of the theoretical curve (curves a, b, c, d & f). After this, the means of the experimental and theoretical distributions were matched.

Lastly, having decided on the best approximation to the form of the parent distribution, the appropriate columns of Table 1 were consulted to give a figure for the ratio of shortfall to standard deviation. From each sample-of-ten from a particular individual, the standard deviation (of the parent distribution) was estimated in the usual way, and then this ratio was used to estimate the shortfall. The shortfall was then added to the highest of the ten measurements to give the ultimate force for each individual.

RESULTS

For the set of 100 observations of beetle mandible forces previously referred to, a good fit with the experimental figures resulted from using the theoretical curve:

$$p = 1/2 \sin \left\{ \frac{\text{Force}^{1.27}}{155.71} - 1.284 \right\}$$

where p. δ (force) is the probability of finding an observation within a small range of forces of width δ (force). Forces are measured in grams-weight. The angle whose sine is taken is permitted to lie within the range 0

to π radians, i.e. forces lie within the range 63.9 to 168.8 grams-weight. For forces outside this range, p = 0. 168.8 g-wt. represents the ultimate force for this specimen. Raising the force to the power 1.27 corrects for skewness in the force-distribution for this individual and this, together with the sine-shape of the probability function, is presumed to be applicable to all individuals. (This assumption was, in fact, checked, by rescaling results for all individuals to a common mean and standard deviation and showing that a similar theoretical curve gave a good fit.) The factor 155.71 ensured that the function inside the bracket had a standard deviation of $\pm$ 0.68, as is necessary for the sine function, while the subtrahend of 1.284 brings the mean of the quantity within the bracket to $\pi/2$. The figure of 155.71 will, of course, change when the sine fuction is matched to the observations from other individuals. The subtrahend plays no part in the subsequent calculations.

Table 2 shows, in the first column of figures, the forces measured in the strongest of 10 nips by 76 individuals alongside, in the second column of figures, the unbiased estimate of the ultimate possible force exertable by each individual under the conditions of the original experiment, the calculations having been made by the methods above.

DISCUSSION

Among the sources of error in this method, a large one is the sampling error inherent in using only the highest observation of ten as the basis. The last column of Table 1 shows the coefficient of variability for this when considered as a sample from a parent distribution of known mean and standard deviation. It may be objected that the outcome of adding the estimated shortfall to an experimental result is merely to replace a systematic shortfall by a random error that is nor much smaller than the systematic one that it replaces. But judgments are unlikely to be made ˙on the basis of measurements from a single individual, and averaging comparable results from several individuals will mitigate the effect of a random error but not that of the systematic shortfall.

There is much more of statistical interest concerning these distributions with an upper limit than merely the estimation

Table 2

Maximum measured mandibular forces and estima-
ted ultimate forces for 76 individual adult passalid beetles.

Species	Maximum measured force (g-wt.)	Estimated ultimate force (g-wt.)	Species	Maximum measured force (g-wt.)	Estimated ultimate force (g-wt.)
Didimus alvaradoi Baguena			*Odontotaenius striatopunctatus* (Perch.)		
	74	78		221	240
	61	65		182	194
Erionomus pilosus Auriv.			*Oileus heros* (Truqui)		
	156	170		355	399
	178	198	*Oileus rimator* (Truqui)		
	203	223		83	90
	170	182		167	178
	234	256		146	162
	183	197	*Passalus punctatostriatus* Percheron		
Erionomus planiceps (Eschscholtz)				49	55
	458	495	*Petrejoides orizabae* Kuwert		
	443	489		88	98
	514	574	*Proculejus brevis* (Truqui)		
	453	489		209	244
	427	466		139	160
	304	330		262	313
	430	469		205	234
	380	421		352	401
	269	293		288	336
	434	459		156	180
	365	390		201	223
	360	377		171	187
Heliscus tropicus (Percheron)				171	200
	109	120		193	212
	106	118		305	340
	61	70		269	300
	103	112		310	330
	173	187		350	386
	152	169	*Proculus beckeri* (Zang)		
	158	171		1015	113C
	121	127		566	640
	196	223		897	969
	208	225		716	786
	219	247	*Pseudacanthus mexicanus* (Truqui)		
Heliscus Vazquezae Reyes-Castillo y Castillo				150	173
	231	252		254	286
	343	374		200	220
	119	136		128	139
	89	97		173	187
	237	254		203	221
	263	278	*Spurius halffteri* Reyes-Castillo		
	288	321		27	30
	170	188		36	39
				53	57
				61	68

of the ultimate performance. For example, it is often an easy matter to devise statistical tests and tables, to allow the use of the estimates of ultimate performance as a criterion of whether two, say, samples-of-ten have been drawn from the same parent population. This is valuable because ultimate performance may well be a biologically-determined quantity in circumstances where mean and standard deviation of a sample-of-ten might depend on changeable or unknown vagaries of measurement technique.

Finally, a mention may be made of the widespread possible value of measures of ultimate performance. In evolutionary terms, it seems possible that survival of individuals of a species could frequently depend on their ultimate performances in life-or-death situations, rather than on average performances. Seen in this light, estimates of ultimate performance acquire considerable interest. It is therefore surprising that standard statistical texts treat as briefly as they do the matter of such estimations.