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# CAN LANCHESTER'S LAWS HELP EXPLAIN INTERSPECIFIC DOMINANCE IN BIRDS?

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*Abstract.* We studied the applicability of Lanchester's laws of combat to explain interspecific dominance in birds. We focused on 10 species of Australian birds in the arid zone of New South Wales that foraged at an established locust trap. Consistent with the ''linear law,'' larger species usually dominated smaller species in one-on-one encounters. We found no support for the ''N-square law,'' which predicted that large numbers of smaller species could dominate larger species when more abundant. Further analysis of the most abundant species revealed that it was less likely to visit the locust trap when larger, more dominant heterospecifics were present. Body size, and not numerical superiority, seems to be an important determinant in interspecific foraging decisions in birds.

*Key words: body size, foraging behavior, group size, interspecific competition, Lanchester's laws.*

## ¿Puede la Ley de Lanchester Ayudar a Explicar la Dominancia Interespecífica en Aves?

*Resumen.* Hemos estudiado la aplicabilidad de las leyes del combate de Lanchester en explicar la domi-

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nancia interespecífica en aves. Hemos focalizado este estudio en 10 especies de aves australianas de la zona árida de New South Wales, las cuales se alimentaron en trampas de insectos establecidas para tal fin. Consistente con la ‘‘ley lineal,’’ las especies de mayor tamaño usualmente dominaron a las especies más pequeñas en los encuentros uno a uno. No encontramos evidencia que apoye la ‘‘ley cuadrática,’’ la cual predice que un gran número de especies de pequeño tamaño podrían dominar a especies de tamaño mayor cuando las primeras son más abundantes. Posteriores análisis sobre la especie más abundantes revelaron que la probabilidad de visita a las trampas de insectos es menor cuando individuos heteroespecíficos más grandes y más dominantes están presentes. El tamaño corporal, y no la superioridad numérica, parece ser un importante factor en las decisiones de forrajeo en las aves.

Competition for resources within multispecies systems leads to the establishment of dominance hierarchies in which certain species outcompete others (Wallace and Temple 1987, Travaini et al. 1998, Sandlin 2000). In some cases, body size is the primary factor that determines interspecific rank (Kohda 1991, Daily and Ehrlich 1994, Bassett 1995, McGlynn 2000). However, in other instances, the relative number of individuals, independent of body size or behavior, may affect interspecific dominance (Basset 1997, Burger and Gochfeld 1984, Creel 2001, Chapman and Kramer 1996, McGlynn 2000).

The study of human warfare has led to the development of many different military strategies. In 1916, F. W. Lanchester published his theory of combat, which included two mathematical models which have become known as the ‘‘linear law’’ and the ‘‘N-square law’’ (Lanchester 1916). The linear law predicts that in one-on-one combat, the stronger (i.e., larger) individual will win. The N-square law predicts that larger-numbered groups can overcome smaller-numbered groups, with differences in individual body size being of little or no importance. Aside from military applications, small businesses have used Lanchester’s strategies to take over markets dominated by larger business (e.g., Yano 1995), a scenario which is at least superficially much like animals competing for access to a limited resource. Recently, biologists have begun to test the applicability of these laws to a variety of animal species engaged in mortal combat. In 1993, Franks and Partridge were the first to show that Lanchester’s models could explain the outcome of interactions among slave-making and army ants. Additional studies of interspecific competition among ants (McGlynn 1999, 2000) provide further support for the linear and N-square laws. Intraspecific interactions among ants (Whitehouse and Jaffe 1996), as well as between chimpanzee groups (Wilson et al. 2002), also follow the predictions Lanchester set forth. In these studies, larger individuals dominated smaller individuals in one-on-one lethal combat (Lanchester’s linear law), and greater numbers of individuals dominated fewer numbers regardless of individual body size (Lanchester’s N-square law).

We observed the behavior of birds foraging for insects at a locust trap in the arid zone of southeastern Australia. We studied interspecific interactions to determine the effect of (1) species type, (2) body size, and (3) abundance on interspecific dominance rank. In doing so, we evaluated Lanchester’s law’s ability to explain nonfatal aggression and dominance in this assemblage. Although the interactions between these species are not immediately lethal, the ephemeral and patchy nature of resources in the arid zone increase the importance of locating and obtaining food. Should interspecific interactions interfere with an individual’s ability to obtain food, we can envision a large fitness cost.

## METHODS

We observed birds foraging at an insect light trap set up by the Australian Plague Locust Commission for monitoring and researching plague locusts on the Fowler’s Gap, New South Wales sheep station (31°5′S, 142°42′E). This locust trap, though technically an artificial food source for birds in the area, was in operation from 1976–1988, and 1994 to present. The trap consisted of a 3.0-m-diameter circular metal tub positioned 0.6 m above the ground and filled with 0.15 m of water. Trees and brush were present nearby. We positioned ourselves on a platform 22.3 m from the locust trap. Directly above the center of the tub, a bright light was turned on nightly. Insects, most commonly moths (Order Lepidoptera), were drawn to and disoriented by the light, whereupon they fell into the water and collected on the surface. Additionally, a large number of water insects such as water-boatmen and backswimmers (Hemiptera) and diving beetles (Coleoptera) inhabited the trap. Although the relative abundance of insects in the trap seemed to vary each morning, a variety of insects were present each day. All observed bird species foraged on these insects on multiple occasions, although not all were exclusively insectivorous (e.g., honeyeaters).

During 53 hr of morning observations between 21 April and 3 May 2001, we continuously recorded every dominant–subordinate interspecific interaction that occurred at the locust trap as a win or a loss. At the time of the interaction, the recorder noted the species of the winner and loser, the time of the interaction, and the number of other individuals of each species present at the trap. Presence was predefined as being perched atop or inside the main tub of the trap or the light canister, flying in the immediate airspace, (within 0.3 vertical m of the surface of the trap), or sitting atop a small post connected to one edge of the tub. Dominant-subordinate interactions consisted of pecking at, chasing, supplanting, or any other interactions in which the subordinate individual of one species moved away as a direct result of the dominant individual of a different species’ actions. We took care to avoid recording what appeared to be coincidental, simultaneous departures from the locust trap, as well as departures that were potentially attributable to external disturbances.

In order to ascertain which species were likely to interact, and to calculate the overall rate of species visitation, we also took an instantaneous census of the

TABLE 1. Body size and mass hierarchy for insectivorous birds foraging at a locust trap in New South Wales, Australia. Body sizes are midpoints of ranges reported in Pizzey and Knight (2001). Average body masses are from Geffen and Yom-Tov (2000), except for Yellow-throated Miner and White-plumed Honeyeater (Higgins et al. 2001), Spiny-cheeked Honeyeater (Casotti and Richardson 1992), and Singing Honeyeater (Wooler et al. 1985).

| Species | Body size (cm) | Body mass (g) |
|---|---|---|
| Australian Raven (*Corvus coronoides*) | 50.0 | 674.5 |
| Australian Magpie (*Gymnorhina tibicen*) | 41.0 | 322.8 |
| Apostlebird (*Struthidea cinerea*) | 31.0 | 130.0 |
| Magpie-lark (*Grallina cyanoleuca*) | 28.0 | 80.0 |
| Yellow-throated Miner (*Manorina flavigula*) | 26.3 | 55.0 |
| Spiny-cheeked Honeyeater (*Acanthagenys rufogularis*) | 24.0 | 44.0 |
| Willie Wagtail (*Rhypidura leucophrys*) | 20.5 | 19.0 |
| Restless Flycatcher (*Myiagra inquieta*) | 18.5 | 15.0 |
| Singing Honeyeater (*Lichenostomus virescens*) | 20.0 | 19.0 |
| White-plumed Honeyeater (*Lichenostomus penicillatus*) | 16.0 | 18.5 |

number of each species present at the trap every 2 min. From the preliminary observations, we determined that a 2-min interval gave the most reasonable overview of the dynamics of bird visitation to the trap. In addition, at the beginning of every hour, the current weather conditions and temperature were recorded.

We standardized the census data by dividing the 6-hr observation window into three 2-hr periods (06:00–08:00, 08:01–10:00, 10:01–12:00) based upon natural divisions in a plot of species abundance over time. Then, for these three time intervals, we divided the number of birds of each species by the total number of observation points to obtain the rate of visitation of each species for each interval. From this, we were able to see what species were rarely or never present at the same time, exclude them, and develop a subhierarchy for each period. Ten avian species (Table 1; scientific names therein) visited the trap during our period of observation and were used for our statistical analyses. These 10 species were all observed foraging on dead insects in the trap on multiple occasions. We removed a single interaction where a Restless Flycatcher very aggressively mobbed an Australian Raven because mobbing is not a typical foraging behavior.

### STATISICAL ANALYSES

To test the applicability of Lanchester's linear law to this group of birds, we compared whether the dominance patterns exhibited at the food source matched the size hierarchy we created by comparing body size (cm) and mass (g) of the species. To quantify dominance at the trap, we input the win-loss data into the program Peck Order (Hailman 1994) to create an overall hierarchy spanning the entire observation period. To determine whether body size explained significant variation in dominance ranking, we calculated Spearman rank correlations of rank versus the midpoint of the body length and rank versus average mass. Throughout, we interpret $P < 0.05$ as significant.

We calculated subhierarchies during each of the three census periods and excluded uncommon species until we obtained a linear hierarchy (Landau's $h = 1.0$; Lehner 1996). For period 1, we first excluded Singing Honeyeater because they were never present during that period, and then excluded Australian Ravens, Spiny-cheeked Honeyeaters, and White-plumed Honeyeaters because certain dyadic encounters with these species did not occur. To create a linear hierarchy in period 2, we excluded Australian Ravens because they were not present during that period, and then Spiny-cheeked Honeyeaters, Singing Honeyeaters, and White-plumed Honeyeaters. To create a linear hierarchy in Period 3, we excluded Australian Ravens because they were never present, and then Spiny-cheeked Honeyeaters, Yellow-throated Miners, Apostlebirds, and Australian Magpies.

In addition, because Willie Wagtails were present more often than any other species and were also present throughout the entire observational period, we were able to use a contingency table analysis to determine whether the time Willie Wagtails spent at the feeder was influenced by the presence or absence of other birds.

To test the applicability of Lanchester's N-square law, we determined whether the presence or number of potential competitors influenced the outcome of an encounter. We fitted logistic regressions using StatView 5.1 (SAS Institute 1999) to estimate the variation explained by group size on the likelihood that an individual of a species would win or lose an interaction with another species. Species-pairs were selected based on the number of observations.

## RESULTS

### LINEAR LAW

Our overall hierarchy, compiled from the win-loss data for the 10 species feeding on the locust trap, was not strictly linear (Table 2). Although not all of the 10 species had the same likelihood of being seen at the same times at the trap, causing certain dyadic encounters to be either missing or tied in our data set, the overall best-fit dominance hierarchy followed the body-size hierarchy (Table 1).

When we focused on birds regularly present at the same time, dominance rank was positively correlated with body size. For both period 1 and period 2, the hierarchy was, from most dominant to most subordi-

TABLE 2. Interspecific dominance matrix for 10 bird species foraging at a locust trap in New South Wales, Australia. Species are arranged by body size. Winners are listed down the left column; losers are listed across the upper row. Values within the matrix represent the number of occurrences of each win-loss dyad. Not all possible dyadic interactions occurred; the matrix reflects the best-fit hierarchy.

| | Losers | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Winners | Aust. Raven | Aust. Magpie | Apostle-bird | Magpie-lark | Y-thrtd. Miner | Sp-ch. Honey-eater | Willie Wagtail | Fly-catcher | Singing Honey-eater | Wh-pl. Honey-eater |
| Australian Raven | — | 6 | 7 | 2 | 0 | 0 | 0 | 0 | 0 | 0 |
| Australian Magpie | 0 | — | 28 | 18 | 15 | 1 | 12 | 4 | 0 | 0 |
| Apostlebird | 0 | 1 | — | 22 | 11 | 0 | 24 | 5 | 0 | 0 |
| Magpie-lark | 0 | 0 | 8 | — | 11 | 6 | 45 | 27 | 1 | 6 |
| Yellow-throated Miner | 0 | 0 | 0 | 0 | — | 1 | 5 | 1 | 0 | 0 |
| Spiny-cheeked Honeyeater | 0 | 0 | 0 | 0 | 0 | — | 4 | 1 | 0 | 1 |
| Willie Wagtail | 0 | 0 | 1 | 0 | 1 | 0 | — | 5 | 8 | 2 |
| Restless Flycatcher | 0 | 0 | 0 | 1 | 0 | 0 | 4 | — | 3 | 5 |
| Singing Honeyeater | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | — | 7 |
| White-plumed Honeyeater | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 3 | — |

nate, Australian Magpies, Apostlebirds, Magpie-larks, Yellow-throated Miners, Willie Wagtails, Restless Flycatchers (Table 3). For period 3, the hierarchy was Magpie-larks, Willie Wagtails, Restless Flycatchers, Singing Honeyeaters (Table 4). All three of these hierarchies were linear with a Landau's $h = 1$. The midpoints of species body length ($r_s = 0.99$, $P < 0.001$) and average body mass ($r_s = 0.95$, $P < 0.001$) were both highly correlated with rank.

The presence of Willie Wagtails was significantly affected by the presence or absence of other species at the locust trap ($\chi^2_1 = 6.1$, $P = 0.01$). Out of 1733 censuses, Willie Wagtails were present during 220. Of these, Willie Wagtails were present at 154 censuses when other species dominant to Willie Wagtails were absent, but were present at only 66 censuses when other species dominant to Willie Wagtails were present. Of the 1513 censuses at which Willie Wagtails were absent, there were 1173 censuses where species dominant to Willie Wagtails were absent as well and 340 censuses where species dominant to Willie Wagtails were present. Willie Wagtails were more likely to be present at the locust trap in the absence of other more dominant birds.

### N-SQUARE LAW

Of the 10 logistic regressions, only the Apostlebirds versus all others visiting the feeder showed any significant association between group size and dominance ($P < 0.001$, Table 5). This relationship was, however, negative: as Apostlebird numbers increased, their likelihood of dominating other species decreased.

## DISCUSSION

Body size in this particular group of Australian insectivorous birds was positively correlated with the interspecific dominance relationships we observed at Fowler's Gap. The species that dominated more often were those that had a larger overall body size. This supports Lanchester's linear law in that larger species will dominate smaller species in one-on-one interactions.

Further support for the linear law is seen in our analysis of how the presence or absence of Willie Wagtails was influenced by other species. Willie Wagtails were significantly less likely to be at the locust trap when an individual of a larger, more dominant species was present. This suggests that the different bird species might have used the presence and size of other species

TABLE 3. The unique linear hierarchy of species foraging at a locust trap in New South Wales, Australia, during periods 1 (06:00–08:00) and 2 (08:01–10:00). Species are arranged by body size. The species compositions and dominance rankings were the same for these two periods; therefore we combined these numbers into a single matrix. Landau's $h = 1$.

| | Losers | | | | | |
|---|---|---|---|---|---|---|
| Winners | Magpie | Apostlebird | Magpie-lark | Y-thrtd. Miner | Willie Wagtail | Flycatcher |
| Australian Magpie | — | 28 | 18 | 15 | 12 | 4 |
| Apostlebird | 1 | — | 22 | 11 | 24 | 5 |
| Magpie-lark | 0 | 8 | — | 11 | 45 | 27 |
| Yellow-throated Miner | 0 | 0 | 0 | — | 5 | 1 |
| Willie Wagtail | 0 | 1 | 0 | 1 | — | 5 |
| Restless Flycatcher | 0 | 0 | 1 | 0 | 4 | — |

TABLE 4. The unique linear hierarchy of species foraging at a locust trap in New South Wales, Australia, during period 3 (10:01–12:00). Species are arranged by body size. Landau's $h = 1$.

| | Losers | | | | |
|---|---|---|---|---|---|
| Winners | Magpie-lark | Willie Wagtail | Restless Flycatcher | Sp-ch. Honeyeater | Wh-pl. Honeyeater |
| Magpie-lark | — | 45 | 27 | 1 | 6 |
| Willie Wagtail | 0 | — | 5 | 8 | 2 |
| Restless Flycatcher | 1 | 4 | — | 3 | 5 |
| Spiny-cheeked Honeyeater | 0 | 3 | 0 | — | 7 |
| White-plumed Honeyeater | 0 | 1 | 0 | 3 | — |

present at the locust trap when deciding whether to land and forage (Daily and Ehrlich 1994). These patterns of interspecific social interactions or avoidance can influence both the instantaneous and long-term distributions of birds in a given area. Thus, pairwise dominance relationships may explain the development of different ecological niches, as well as resource partitioning (Fisler 1977, Nagamitsu and Inoue 1997).

However, we found no support for Lanchester's N-square law with our data. Group size was not a significant factor in influencing interspecific dominance interactions among the 10 bird species that fed at the locust trap. Of the 10 logistic regressions we ran, only one was significant. For some of the pairings, the lack of significance may result from a paucity of data. The negative relationship in the one significant regression is further evidence against Lanchester's N-square law. The N-square law also may not apply to these birds due to the lesser degree of cooperation seen in flocks or gatherings of birds as compared to humans, chimpanzees, or ants.

The birds foraging at the locust trap were concentrated around an abundant food source. Thus, it is reasonable to assume that the same dominance relationships identified in our study are likely to apply at concentrated food patches throughout the arid zone.

In conclusion, while it seems that both of Lanchester's laws have great explanatory value for potentially fatal combat among ants and chimpanzees, the N-square law has limited ability to explain the nonfatal interspecific dominance hierarchies in at least one group of Australian insectivorous birds. These specific findings may have applicability to a much broader understanding of behavioral interactions among species inhabiting a common habitat and sharing some or all of the same resources.

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TABLE 5. Summary of the logistic regression models that explained the probability that a given species would win an encounter given the group size of its competitor. Group sizes are means ± SD. Full common names appear in Table 1.

| Species 1 | | | | Competitor | | | |
|---|---|---|---|---|---|---|---|
| Species | Group size | No. of wins | No. of losses | Species | Group size | $P$ | $R^2$ |
| Apostlebird | 6.3 ± 3.3 | 1 | 28 | Austr. Magpie | 1.6 ± 0.5 | 0.15 | 0.44 |
| Austr. Magpie | 1.7 ± 0.5 | 18 | 0 | Magpie-lark | 1.1 ± 0.3 | | |
| Magpie-lark | 1.3 ± 0.5 | 8 | 22 | Apostlebird | 3.6 ± 1.8 | 0.97 | 0.002 |
| Apostlebird | 4.6 ± 2.9 | 63 | 44 | all species[a] | 1.9 ± 0.9 | $<0.001$ | 0.10 |
| Austr. Raven | 1.5 ± 0.5 | 15 | 0 | all species[a] | 4.6 ± 3.2 | | |
| Austr. Magpie | 1.5 ± 0.5 | 78 | 7 | all species[a] | 3.9 ± 3.0 | 0.27 | 0.03 |
| Magpie-lark | 1.3 ± 0.5 | 104 | 43 | all species[a] | 2.7 ± 2.0 | 0.06 | 0.02 |
| Sp-ch. Honeyeater | 1.2 ± 0.5 | 10 | 15 | all species[a] | 1.8 ± 1.3 | 0.20 | 0.05 |
| Wh-pl. Honeyeater | 1.9 ± 1.4 | 4 | 21 | all species[a] | 1.9 ± 0.9 | 0.39 | 0.03 |
| Y-thrtd. Miner | 1.9 ± 1.2 | 7 | 38 | all species[a] | 2.8 ± 2.7 | 0.12 | 0.06 |

[a] All other species present during species 1's interactions.

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