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# Competitive inter- and intraspecific dominance relations in three gull species

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Yellow-legged *Larus michahellis*, Audouin's *Ichthyaetus audouinii* and Black-headed Gulls *Chroicocephalus ridibundus* are common species in the western Mediterranean where they coincide spatially and temporally. Competition for food resources leads to agonistic interactions, which we predict will have a hierarchical structure following Lanchester's linear law. We recorded the behaviour of these three species in feeding and non-feeding contexts in wild populations in the city of Barcelona and its metropolitan area. We found both age-structured intraspecific dominance and size-based interspecific dominance in hierarchical tendencies that support the predictions of Lanchester's law. Dominance interactions mostly consisted of low-intensity aggressive behaviour. Agonistic interactions were more frequent when feeding, which suggests that individuals may risk more costly interactions to gain access to valuable resources.

Key words: Yellow-legged Gull, *Larus michahellis*, Audouin's Gull, *Ichthyaetus audouinii*, Black-headed Gull, *Chroicocephalus ridibundus*, animal behaviour, western Mediterranean.

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Dominance interactions are a universal phenomenon in animal relationships (Allee 1938). When species compete for the same resource, dominance interactions occur between individuals, which can lead to the establishment of temporary interspecific dominance hierarchy systems (Minock 1972, Fisler 1977, Wallace & Temple 1987, Travaini *et al.* 1998, Sandlin 2000, Shelley *et al.* 2004).

Lanchester (1916) defined a 'linear law' whereby a lethal one-on-one combat will lead to the success of the largest and therefore the strongest individual. Some studies sustain that Lanchester's linear law also helps predict the outcome of non-deadly dominance interactions under a scenario of interspecific competition (Whitehouse & Jaffe 1996, McGlynn 1999, 2000; Wilson *et al.* 2002, Adams & Mesterton-Gibbons 2003, Shelley *et al.* 2004, Chock *et al.* 2018) since the largest of the competitors will scare off and dominate the others by sheer dint of size.

Contestants use different strategies in dominance interactions. The most aggressive strategies allow individuals to dominate in an interaction but are costly in terms of energy, time and risk of injury (Smith & Prince 1973). In extreme forms, aggressiveness can even lead to death. Alternatively, individuals who avoid such risks by displaying no aggressiveness at a resource will lose out to aggressive competitors, especially when the resource is scarce (Sirot 2000). Thus, aggressiveness is a trade-off influenced by resource availability (Kotrschal *et al.* 1993, Dolman 1995, Smith & Metcalfe 1997, Roff & Fairbairn 2007). Optimal benefits are often found when animals are fairly aggressive, even at low population densities. When the resource availability decreases or a particular resource is highly valuable, individuals can increase their aggressiveness threshold (Sirot 2000). Trade-offs that take into account benefits and the costs of competitive interactions also explain why this type of behaviour is or

is not apparent (Roff & Fairbairn 2007). As a result, animals have developed strategies and conventions through which dominance interactions can be resolved without physical combat (Parker 1974).

A 'prior attributes' hypothesis states that hierarchical relationships based on phenotypic criteria are formed between individuals, whose physical attributes will predetermine their position in a hierarchy (Chase *et al.* 2002). Moreover, in a dominance interaction, differences in an individual's attributes (e.g. body size, age or plumage colouration) reflect their dominance ability and so can be used to avoid highly costly aggressive interactions (Rowell 1974).

In recent decades, several gull populations have expanded in Europe (Vidal *et al.* 1998). The Yellow-legged Gull *Larus michahellis* is becoming commoner in the Mediterranean basin and is found there throughout the year. Audouin's Gull *Ichthyaetus audouinii* is found during the breeding season in the Mediterranean basin but mostly winters in western Africa. The Black-headed Gull *Chroicocephalus ridibundus* is mainly a winter species in the Mediterranean basin, although some breeding colonies are known (Svensson *et al.* 2009, Olsen & Larsson 2010). These three species overlap in the western Mediterranean and usually feed on similar food resources. The Yellow-legged Gull is a generalist predator that usually feeds on human-generated resources (Duhem *et al.* 2003, Ramos *et al.* 2009). Likewise, Black-headed Gull is also known to feed on this type of resource (Vernon 1972, Scott *et al.* 2015). Audouin's Gull, on the other hand, has modified its behaviour in recent years and now feeds more on anthropically generated food sources (Arcos *et al.* 2001, Pérez Jiménez 2014).

The Yellow-legged Gull is a competitor and predator of other seabird species and can even affect their population trends (Oro *et al.* 2005, Skórka *et al.* 2012). Yellow-legged Gull kleptoparasitism, as well as predation on Audouin's and Black-headed Gull eggs, nestlings and adults, have been reported from many sites (Oro *et al.* 1994, Lambertini 1996, Arcos 2001, Martínez-Abraín *et al.* 2003, Skórka *et al.* 2012).

Our objective was to determine the dominance relationships established between these three gull species. For this purpose, we compared their behaviour under feeding and non-feeding competition scenarios via an observational study of their interactions. In particular, we studied: 1) *Intraspecific hierarchy relations* by comparing juvenile vs adults since older and more experienced individuals are predicted to be more dominant; 2) *Interspecific hierarchy relations* by studying Yellow-legged vs Audouin's vs Black-headed Gull interactions since larger individuals are expected to most often be the aggressors and dominant birds in interactions; 3) *Feeding context as a keystone of dominance relations* by comparing agonistic interactions in the presence or otherwise of food since the availability of resources is expected to increase the aggressiveness of individuals; 4) *Optimal intensity distribution of dominance relations* by analysing the intensity of agonistic interactions since low intensity behaviour is expected to be preferred as a means of avoiding severe costs (e.g. injuries).

## Material and methods

We observed gulls at six sites in Barcelona and its metropolitan area in February–April 2018 and 2019. Three sites were large urban parks with ponds (Parc de l'Espanya Industrial: 41°22'N 2°08'E; Parc de la Ciutadella: 41°23'N 2°11'E; UPC Campus in Castelldefells: 41°16'N 1°58E), while the other three were on the coast (Moll de Drassanes: 41°22'N 2°10'E; Platja de Sant Miquel; 41°22'N 2°11'E; Platja de Castelldefells 41°15'N 1°57'E). We selected these locations because we had previous observational evidence that the studied gull species co-occur there, which made it possible to observe interactions. We pooled all observations as we considered that site identity was not relevant to our behavioural approximation and, indeed, the species composition and the interactions recorded did not differ markedly between the study sites.

**Table 1.** Number of individuals per register. SD = Standard deviation.
*Nombre d'individus per registre. SD = desviació estàndard.*

| **Group** *Grup* | **Mean** *Mitja* | **SD** *SD* | **Range** *Rang* |
|---|---|---|---|
| Yellow-legged Gull (adults) | 4.43 | 1.55 | 3 - 8 |
| Yellow-legged Gull (juveniles) | 4.57 | 1.74 | 2 - 8 |
| Black-headed Gull | 22.64 | 7.21 | 12 - 41 |
| Audouin's Gull | 1.26 | 2.23 | 0 - 6 |

Three *Laridae* species were studied: Yellow-legged, Audouin's and Black-headed Gulls. In spite of the fact that intraspecific interactions could have been studied in all species given the easily distinguishable phenotypes of immature and adult birds, we were only able to do so in the Yellow-legged Gull. In the Black-headed Gull, intraspecific behaviour observations were not possible due to the large numbers of individuals of this species in the monitored groups (see Table 1), while for Audouin's Gull, no juvenile individual was observed. In the Yellow-legged Gull, we classified as juveniles all birds up to third-year plumages (Olsen & Larsson 2010) and as adults any older bird.

Data was collected in a multifocal real-time approximation, which also included considerations of other competitive feeding agonistic behaviour surveys such as Burguer's *aggressive interactions* highlights (1981). We set up alternatively two recording scenarios: feeding and non-feeding. First, the observer provided approximately 250 gr of bread (i.e. food) 10 m from his position. Bread was thrown out just before the start of a trial. Recording started when the first gulls interacting with the food appeared. During two minutes (feeding context), we recorded all observed intra- and interspecific agonistic interactions. Once the bread run out, the observer began a new behavioural record of 2 minutes (non-feeding context) at the same place. If no gull was attracted in a period of 4 minutes after the bread was provided, the trial ended. This happened in 45% of cases. We carried out only one register per day and per site to avoid pseudoreplication (i.e. observation of the same individuals) and dependencies (behaviour conditioned by previous trials).

Agonistic interactions were scaled for intensity in three categories adapted from Tinbergen's *Laridae* behavioural studies (Tinbergen 1960). High intensity behaviour consisted of *aggression,* which involved physical contact, pecking or striking both in aerial persecutions and on the ground. Moderate intensity corresponded to *displays*, that is, displays of strength consisting of short and ritualized approaches with upraised wings and fast swinging moves, sometimes involving vocalizations. Low intensity behaviour was simple *displacement*, defined as the withdrawal from a resource spatially and/or stopping feeding when another individual arrived that might or not exploit this resource.

We did not consider how one behaviour affects an immediately posterior behaviour, that is, we did not determine possible dependencies between sequential behaviours as it was impossible to identify individually each bird. We realize this is a drawback since recorded interactions can be non-independent, which violates basic assumptions of statistical tests. However, we believe that the large number of observations conducted at several different sites, as well as the number of fieldwork days and years, reduces the importance of this pseudoreplication issue. In addition, the significance threshold was established at $p = 0.005$.

Statistical analyses were conducted with R software v 3.4.0 (R Core Team 2017). We used Generalized Lineal Models (GLM) with Poisson distribution to test how the number of interactions (response variable) differed 1) between adult and juvenile Yellow-legged Gulls, 2) between the three studied gull species, 3) between feeding and non-feeding contexts, and 4) according to the behavioural intensity and the intra-interspecific type of interaction.

The intra- and interspecific dominance hierarchy in the studied species was established by considering a category (defined by species or age) that was dominant over another whenever the amount of provoked dominance interactions towards a different category was significantly higher than the received dominance interactions from that specific category.

## Results

We recorded 527 agonistic interactions in 44 successfully completed registers. The Black-headed Gull was the most abundant species; adult and juvenile Yellow-legged Gulls occurred in similar numbers (Table 1). Audouin's Gull did not appear in many registers and was the least abundant.

In Yellow-legged Gulls, the average number of adult agonistic interactions over juveniles per register trebled those in the opposite direction (Figs. 1 and 2A). Therefore, adults clearly dominated over juveniles (GLM intraspecific interactions: $F = 34.39$, d.f. $= 86$, $p < 0.001$).

Yellow-legged Gulls, irrespective of their age, were dominant over Black-headed Gulls (GLM

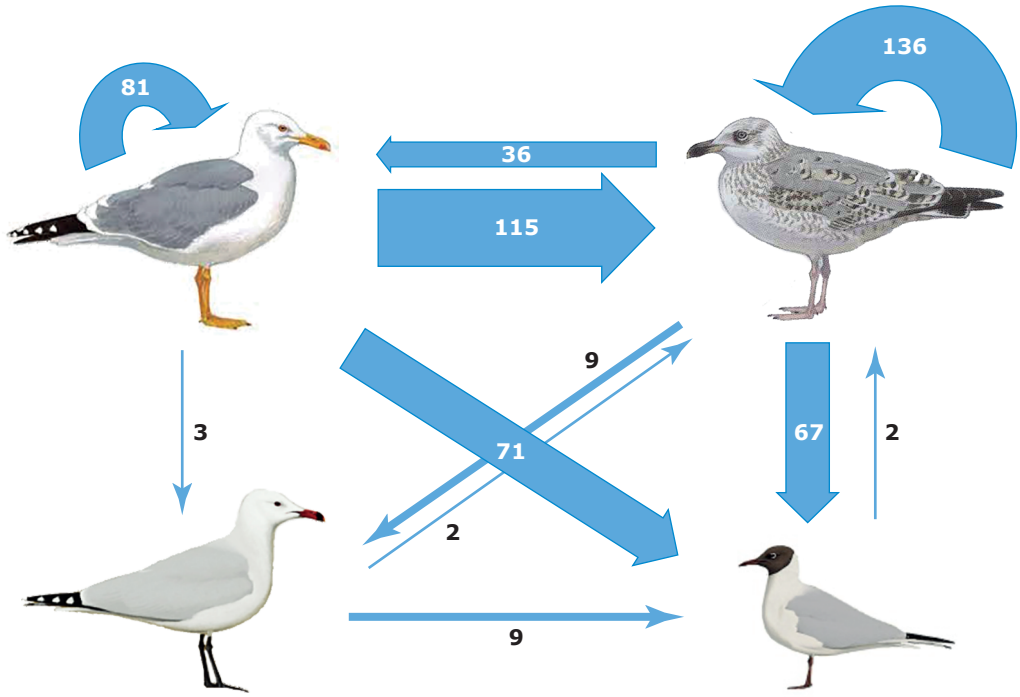


**Figure 1.** Number of agonistic interactions recorded between gull categories. Intraspecific interactions between Black-headed Gulls were not recorded. There were no intraspecific interactions between Audouin's Gulls.
*Nombre total d'interaccions agonístiques enregistrades entre les categories de gavines. Les interaccions entre gavines rialleres no es van enregistrar. No es va observar cap interacció entre gavines corses.*

interspecific interactions: $F = 171.9$, d.f. = 78, $p < 0.001$). The dominance of Yellow-legged Gulls was complete, as Black-headed Gulls almost never made agonistic movements towards Yellow-legged Gulls (mean = 0.05, SD = 0.22; Fig. 2B). Indeed, most of the agonistic behaviour recorded during the registers were of Yellow-legged towards Black-headed Gulls (mean = 3.13, SD = 2.06) (Figs. 1 and 2B). Audouin's Gull was dominant over Black-headed Gull (GLM interspecific interactions: $F = 29.29$, d.f. = 18, $p < 0.001$) but was dominated in turn by Yellow-legged (GLM interspecific interactions: $F = 10.28$, d.f. = 24, $p = 0.004$) (Fig. 1).

The number of agonistic interactions was significantly higher in feeding (mean = 10.68, SD = 4.23) than in non-feeding contexts (mean = 1.36, SD = 2.11) (GLM feeding context: $F = 145.65$, d.f. = 86, $p < 0.001$; Fig. 2C) due to the fact that in the non-feeding context there were no agonistic interactions in most registers, while in the feeding context there was always some degree of aggressiveness between individuals (Fig. 3).

*Displacement* was the most frequent agonistic interaction, followed by *display* and *aggression* (GLM behaviour intensity: $F = 59.56$, d.f. = 262, $p < 0.001$; Fig. 4). Intraspecific agonistic behaviours were also significantly more common than interspecific ones (GLM interaction type: $F = 42.14$, d.f. = 260, $p < 0.001$; Fig. 4). Interestingly, the distribution of the intensity of agonistic behaviour differed between inter- and intra-specific interactions (GLM intensity*type: $F = 12.36$, d.f. = 258, $p < 0.001$; Fig. 4).

## Discussion

Adult Yellow-legged Gulls were dominant over conspecific juveniles. This age-structured hierarchy has been observed in other gull species (Bertellotti & Yorio 2001, Galván 2003) and even in passerines within a competitive feeding context (Enoksson 1988, Senar & Camerino 1998). Inexperience could explain the low hierarchical position of juveniles in an intraspecific

context, experience being a key factor explaining the attaining of higher hierarchical positions (Barash *et al*. 1975, Monaghan 1980, Burger 1983, Galván 2003).

The dominance of Yellow-legged and Audouin's Gulls over Black-headed Gulls, along with the dominance of Yellow-legged over Audouin's Gulls, supports the predictions of Lanchester's linear law. Yellow-legged and Audouin's Gulls are bigger than Black-headed Gulls (Svensson *et al.* 2009) and consequently have a higher probability of winning a one-on-one combat. The same happens when Yellow-legged Gulls come into conflict with Audouin's Gulls. Therefore, size turned out to be the key phenotypic character in the studied species for understanding dominance abilities (Rowell 1974). The species with the largest body size and wingspan is the Yellow-legged Gull (52–58, 120–140 cm), followed by Audouin's Gull (44–52, 117–128 cm) and Black-headed Gull (35–39, 86–99 cm) (Svensson *et al.* 2009). This is exactly the same hierarchical order as we observed.

Size provides an informative and honest *a priori* attribute within non-aggressive dominance interactions such as displacements. Previous studies concur with this hypothesis and reveal that Yellow-legged Gulls and even Audouin's Gulls, as large species, are able to displace other species in a territorial context (Oro *et al*. 2009). Moreover, the size dominance hypothesis also appears to explain interspecific dominance interactions (Werner & Gilliam 1984, Choke *et al.* 2018), specifically in raptor territorial dominance (Martínez *et al*. 2008) and interspecific carrion-dominance relations (Moleón *et al*. 2014).

Given that Yellow-legged Gulls hold the highest position in the interspecific hierarchy, with their adults on top, we postulate that adult Yellow-legged Gulls have greater resource-holding potential (Parker 1974). These high-ranking adults displace during resource exploitation lower ranked juveniles, who are forced to develop other foraging strategies. It has been reported that juvenile *Laridae* gulls have different foraging strategies (Marchetti & Price 1989) and are less efficient when foraging than adults, and that their foraging efficiency decreases when adults are present (Ulfstrand 1979). Hierarchical displacement mean that displaced individuals

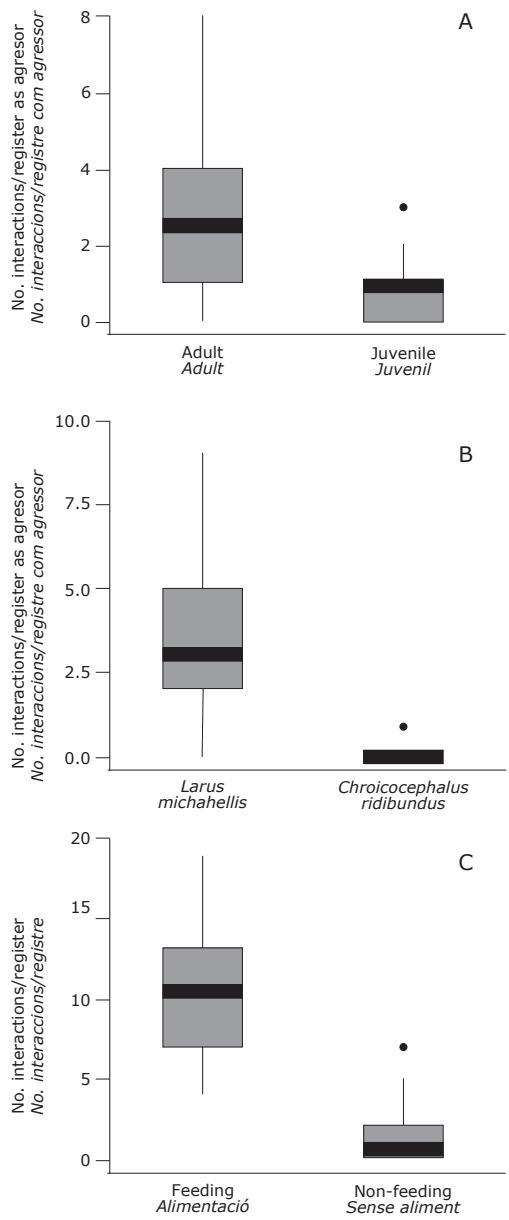


**Figure 2.** Average agonistic interactions per record between different groups of gulls (**A** adult vs juvenile Yellow-legged Gulls; **B** Yellow-legged vs Black-headed Gulls) and in different contexts (**C** feeding vs non-feeding). Boxes represent quartiles, bar intercepts 95% confidence interval, and point intercepts outliers. *Mitjana d'interaccions agonístiques per registre entre diferents grups de gavines (A adults vs joves de gavià de potes grogues; B gavià de potes grogues vs gavina riallera) o en diferents contextos (C alimentació vs sense aliment). Les caixes representen els quartils, la barra l'interval de confiança del 95%, els punts intercepten outliers.*

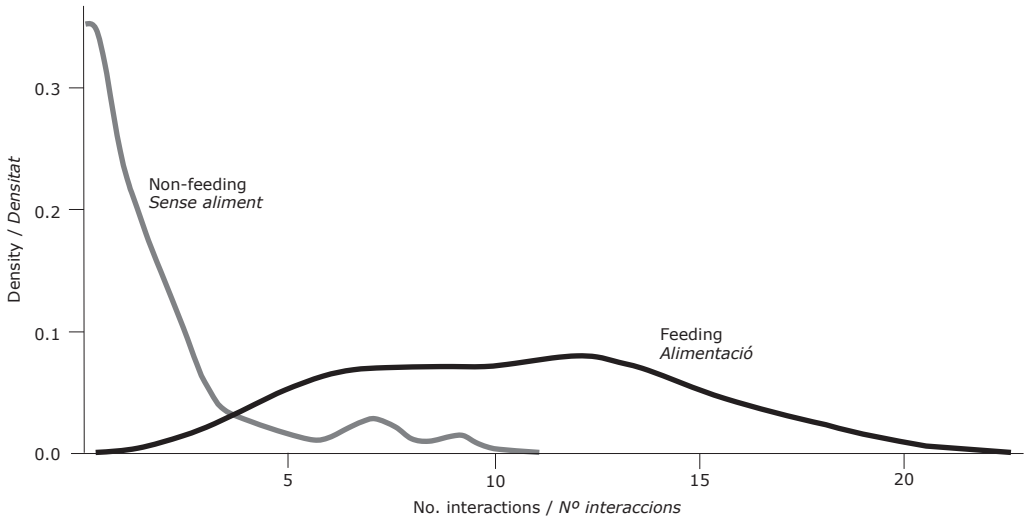


**Figure 3.** Density probability distribution of agonistic interactions in feeding and non-feeding contexts.
*Distribució de les interaccions en un gràfic de densitat considerant el context d'alimentació i sense aliment.*

have to compete directly with other gull species for resources.

Our results coincide with Lanchester's (1916) central idea: larger birds are winners. This can be explained by trade-offs: if size determines the possibilities of defeating other birds in dominance interaction and even can be used to define hierarchy relations, we might also posit that selective forces drive species using aggressiveness as their main strategy to increase in size. Species on the receiving end of this aggressiveness might also benefit from increasing their size. Nevertheless, strategies other than size may be selected for. During the study we observed differing feeding strategies in the three gull species. Although not formally tested, we noted that Black-headed Gulls were usually the first gull to detect, approach and then feed on provided food. Furthermore, Black-headed Gulls took more risks when feeding and had a greater tolerance to human presence, as observed in other studies (Bellebaum 2005). This different feeding strategy may be designed to avoid direct competition (Sol *et al.* 1993) dependent on gull size.

We have demonstrated that feeding contexts are a tool that readily reveals inter- and intraspecific competitive interactions. In presence of a resource such as food, individuals take more risks due to the potential benefits. Feeding contexts have been applied to create high concentrations of individuals (Fisler 1977, Monaghan 1980, Senar & Camerino 1998), which leads to an increase in competitive fighting for a spatially and temporarily limited resource (Monaghan 1980). Therefore, feeding context competition should be considered as a basic tool when studying intra- and interspecific dominance interactions.

Individuals tend to solve dominance interactions preferably by *displacement* behaviour.

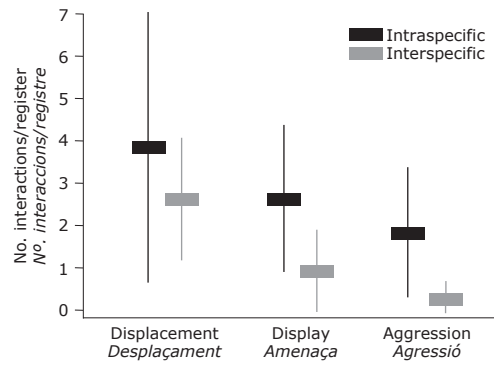


**Figure 4.** Average agonistic interactions of different degrees of intensity between and within species. Error bars show value ranges.
*Mitjana d'interaccions agonístiques per registre de diferent grau d'intensitat entre (interspecific) i dintre (intraspecific) d'espècie. Les barres d'error mostren el rang de valors.*

This agrees with the trade-off approach: the higher the intensity of the dominance behaviour is, the higher the costs and risks for the individual are (Smith & Prince 1973, Roff & Fairbairn 2007). Aggressive behaviour may cause damage to the aggression instigator and so it may not be the best benefit-cost option. Displacements as low-intensity agonistic behaviour are used preferentially to obtain resources involving fewer risks and costs. Thus, a tendency to avoid aggressiveness is to be expected.

Intraspecific agonistic behaviour overcoming interspecific agonistic behaviour abundance indicates that gulls were more aggressive to conspecifics than to heterospecifics. It has been reported that conspecific individuals are tolerated less than heterospecifics in territorial contexts in raptors (Rico 1999, Martínez *et al*. 2008). Therefore, conspecific individuals are more likely to incite an agonistic behaviour response than non-conspecific individuals. Given that conspecifics interact between each other much more than with heterospecifics, we can assume that there is a higher overlap in resource usage in conspecifics, which implies that the proportion of aggressions may increase intraspecifically. High-intensity agonistic behaviour seems to increase proportionally as competition rises. Significant differences between intra- and interspecific aggressions and displays, along with non-significant differences in displacements, seem to indicate a tendency for interspecific competition to be less strong than intraspecific competition, which ensures that higher intensity behaviour is more often present between conspecifics.

To develop an interspecific hierarchy of western Mediterranean gulls, more data for sympatric species such as Lesser-back Backed Gull *Larus fuscus* or Mediterranean Gull *Ichthyaetus melanocephalus* are necessary. Those studies may help us understand complex population dynamics and even behavioural and morphological evolution patterns in *Laridae*. We suggest that a phylogenetic approach relating interspecific hierarchy interactions with heterospecific taxonomical proximity is required. We hypothesize that closely related species deploy more interspecific agonistic behaviour than non-related species and so expect that larger gulls be dominant over smaller ones.

## Resum

### Relacions de dominància inter- i intraespecífiques en tres espècies de gavines

El gavià de potes grogues *Larus michahellis*, la gavina corsa *Ichthyaetus audouinii* i la gavina riallera *Chroicocephalus ridibundus* són espècies comunes al Mediterrani occidental, on coincideixen espacialment i temporalment. La seva competència pels recursos alimentaris dona lloc a interaccions agonístiques, de les quals es pot predir que s'han d'estructurar de forma jeràrquica seguint la llei lineal de Lanchester. Vam enregistrar el comportament de les tres espècies en individus salvatges en contextos alimentaris i no alimentaris en diversos parcs i platges de la ciutat de Barcelona i la seva àrea metropolitana. En els gavians de potes grogues vam trobar una dominància intraespecífica estructurada per l'edat, de manera que els adults van dominar sobre els juvenils, possiblement com a resultat de la seva major experiència. D'altra banda, també vam observar una dominància interespecífica estructurada per la mida de les espècies, d'acord amb les prediccions de la llei lineal de Lanchester. En concret vam trobar que els gavians de potes grogues van dominar sobre la resta d'espècies, i que la gavina corsa també va dominar sobre la riallera. Quan vam crear experimentalment un context alimentari afegint pa al medi, vam enregistrar un augment significatiu de les interaccions agonístiques, fet que suggereix que els individus duen a terme interaccions més costoses en cas d'un potencial benefici, com és un recurs tròfic. Finalment, vam trobar que les interaccions de dominància basades en comportaments agonístics de baixa intensitat van ser el tipus de relació predominant tant entre com dintre d'espècie.

## Resumen

### Relaciones de dominancia inter- e intraespecíficas en tres especies de gaviotas

La gaviota patiamarilla *Larus michahellis*, la gaviota de Audouin *Ichthyaetus audouinii* y la gaviota reidora *Chroicocephalus ridibundus* son especies comunes en el Mediterráneo occidental, donde coinciden espacial y temporalmente. Su competencia por los recursos alimenticios da lugar a interacciones agonísticas, de las que podemos predecir que deben estructurarse jerárquicamente siguiendo la ley lineal de Lanchester. Registramos el comportamiento de las tres especies en individuos silvestres en contextos alimentarios y no alimentarios en varios parques y playas de la ciudad de Barcelona y su área metropolitana. En las gaviotas patiamarillas encontramos una dominancia

intraespecífica estructurada por la edad, en la que los adultos dominaron sobre los juveniles, posiblemente como resultado de su mayor experiencia. Por otro lado, también observamos una dominancia interespecífica estructurada por el tamaño de las especies, de acuerdo con las predicciones de la ley lineal de Lanchester. En concreto encontramos que las gaviotas patiamarillas dominaron sobre el resto de las especies, y que la gaviota de Audouin también dominó sobre la reidora. Cuando creamos experimentalmente un contexto alimentario añadiendo pan en el medio, registramos un aumento significativo de las interacciones agonísticas, lo que sugiere que los individuos llevan a cabo interacciones más costosas en caso de un potencial beneficio, como es un recurso trófico. Finalmente, encontramos que las interacciones de dominancia basadas en comportamientos agonísticos de baja intensidad fueron el tipo de relación predominante tanto entre como dentro de especie.

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