Dominance hierarchy establishment in the invasive round goby, *Neogobius melanostomus*

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ABSTRACT

Organisms living at high densities may be forced to engage in conflict for access to resources such as food or shelter. When these resources are limited, the outcome of interactions may have important fitness implications. We investigated the behavioural interactions of the invasive Round Goby (*Neogobius melanostomus*) in a shelter-limited environment. Round Goby are benthic fish that utilize rocky shelters for predator avoidance and as reproductive sites in which territorial males defend clutches of eggs. Previous work on this and other species has shown that larger individuals have greater resource holding potential in dyadic interactions. In order to understand the outcome of agonistic interactions in more complex social environments, we observed groups of three goby of the same sex which varied in relative size in an aquarium in which individuals had the opportunity to compete for access to shelters. We predicted that larger goby would behave aggressively towards smaller goby, and outcompete smaller goby for access to shelters. Because males defend shelters while breeding, we also predicted that male goby would compete more aggressively than females over dominance status. We found that larger goby in groups were socially dominant to smaller goby, regardless of sex. Additionally, we found that the largest goby in each group was involved in more aggressive interactions than the second or third largest goby in each group. We found no effect of relative size or sex on aggressive interaction or the emergent dominance relationships. Our findings highlight that aspects of the social environment may limit the opportunity for individuals to establish dominance or establish ownership of resources.

Dominance and dominance hierarchies are amongst the foundational concepts utilized by behavioural ecologists to understand social interactions. Across taxa, dominance is both a cause and consequence in the outcome of social interactions, conflict over resources, and access to mates (Dewsbury, 1982; Kaufmann, 1983; Pusey et al., 1997). Dominance plays a role in the fitness of organisms, and an abundance of work has investigated the mechanisms through which individuals achieve dominance status (Holekamp and Smale, 1991; Øverli et al., 1999). Specifically, research has focused on the acquisition of dominance in dyadic conflict (Beaugrand et al., 1991; Martin et al., 1997; Dugatkin and Druen, 2004; Reddon et al., 2011), as well as the structure and consequence of dominance in larger social networks (Krause et al., 2015; Silk et al., 2017). In the present study, we investigated the formation and structure of dominance hierarchies in the invasive round goby, *Neogobius melanostomus*.

Dominance hierarchies are widespread throughout the animal kingdom. In many species, linear (transitive) dominance hierarchies form (Chase, 1982; Rutbeg (1983)). However, these relationships may become more complex as more individuals are considered. In dyadic interactions, larger individuals are often dominant to smaller individuals. This is frequently attributed to a consequence of size either through greater resource holding potential (RHP) (Lindström, 1991; Gherardi, 2006) or experience as a result of age (Hughes and Strassmann, 1988, Collis & Borgia 1992, Archie et al., 2006). Between individuals of similar size, conflict over dominance is often greatest (McCallum et al., 2017; Groen et al., 2012; Reddon et al., 2011), potentially due to uncertainty in assessing opponents. Certain social species may even modify their growth rate to avoid size-based conflict with conspecifics (Buston, 2003; Heg et al., 2004; Wong et al., 2008).

Metrics of dominance are generally based on patterns of agonistic interactions between individuals (Bayly et al., 2006). Winning or losing dyadic agonistic interactions may influence an individual's success in future conflict (Chase et al., 1994; Schuett, 1996; Hsu and Wolf, 1999; Gherardi and Daniels, 2003; Hsu et al., 2006). Additionally, third

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parties may observe the outcome of conflict within dyads and in turn reevaluate whether to engage with losers or winners (Earley and Dugatkin, 2002; Peake et al., 2002; Engh et al., 2005). The advantages of winning early, disadvantages of losing early, and the benefit of observing conflict as a third-party, all support the notion that the order in which dyadic agonistic interactions are resolved can ultimately influence the eventual dominance structure. Thus, some individuals may be at an advantage if they can establish their dominance status over conspecifics early on, while others may benefit from waiting and deciding whether to engage conspecifics based on the outcome of their prior engagements.

In order to investigate how dominance relationships are established in triadic groups, we introduced three same-sex round goby into novel arenas and documented patterns of agonistic interactions within triads. Fish in our experiment varied in relative size, and we predicted that larger fish would be socially dominant to smaller fish (Sopinka et al., 2010, McCallum et al. 2017), and that agonistic interactions would be more frequent 1) for higher positions in the dominance hierarchy, and 2) for a smaller size difference exists between individuals. We predicted larger fish would have greater access to shelters and spend more time in them. We also predicted that larger fish would establish their dominance status earlier than smaller fish, which we would detect through differences in dominance over the course of the observation. Finally, as male round goby compete for access to territories and shelters, while females do not establish territories for reproductive purposes, we hypothesized sex-specific differences would occur in conflict and dominance hierarchy establishment.

1. Methods

From June 19 to July 22, 2016, we collected round goby via seine, trawl, and angling in the vicinity of Gibraltar Island, Lake Erie. Prior to the experiment, we housed goby in one of two 208 L stock aquaria fitted with power filters and provided a minimum of one day for goby to acclimate before experimentation. These aquaria were maintained at very high densities in order to reduce territoriality (Grant, 1997) and reduce the risk that dominance relationships had already formed between experimental fish. Round goby were fed pellet fish food ad libitum as well as wild zebra mussels while housed in stock aquaria.

Prior to experimentation, we individually wrapped three 37.5 L tanks with black, opaque tarp and collectively surrounded the tank area by black tarp; the area above the tanks was left open for light to enter. We filled these tanks halfway (~20 L) with fresh lake water. We placed two shelters in each tank, one which was "high quality" (fully enclosed) and "low quality" (two sided) shelter (McCallum et al., 2017) to create arenas. A 5-centimeter grid was placed underneath each arena, which was visible from above. GoPro cameras were suspended 1 m above the arenas.

For each trial, we selected three same-sex (N = 39 groups, 117 fish total; 24 male groups, 15 female groups), goby of varying sizes (measured as standard length (SL: from the tip of the snout to the end of the caudal peduncle) Female fish mean: 57.30 ± 2.02 mm, Male fish mean: 79.84 ± 2.85 mm). Fish were netted from both stock tanks haphazardly, such that the specific stock tank a given fish originated from, and whether it had any previous interactions with another fish in the trial was randomized. Prior to introducing fish to the arena we inspected each to confirm sex and to take a SL measurement to confirm we had collected 3 fish of the same sex that were at least 5 mm apart in length (so fish could be visually distinguished in videos). We introduced all three fish to the arena simultaneously, and after a five minute habituation period we began a 60 min observation. Observations were filmed using a GoPro camera mounted above the aquarium; videos were scored by an observer naïve to the sex or specific size differences between fish in each group (although the observer could see that some fish were larger than others). The observer recorded the counts of aggressive [bites, chases, and displacement] and submissive behaviours

[hide, flee], based on the ethogram provided by Sopinka et al. (2010). The observer also froze the video at every 60 s interval of the observation and recorded whether each fish was inside a shelter.

1.1. Animal welfare

While animals in this study engaged in aggressive interactions, these interactions were no greater than those fish would have encountered in stock aquaria or in the wild. The authors were present during all observations and checked on fish in trials frequently. Fish also had access to two shelters during trials which provided visual barriers between individuals and further reduced the possibility of escalated aggression. Escalated aggression occurred infrequently during this study, and while they did not occur, had any escalated bouts of mouth fighting or other aggression which could have resulted in physical damage to fish occurred the authors would have terminated the trial immediately and fish would have been separated from one another. This research was approved by Ohio State's Office of Responsible Research Practices under IACUC protocol number 2008A0110-R2. In accordance with the requirements of our Ohio Division of Wildlife wild animal permit (17–152) all goby were euthanized with an overdose of pH buffered MS-222 followed by cranial severance.

1.2. Statistical analysis

In order to quantify relative dominance, we calculated Dominance Index scores for each individual (Dominance Index = Σaggressive behaviours performed − Σsubmissive behaviours performed; see Aubin-Horth et al., 2007). We then ran a Generalized Linear Mixed Model (GzLM) with Dominance Index as the dependent variable. This model utilized a Poisson distribution with a log link; as some values were negative, Dominance Index scores were transformed by adding the [lowest value + 1] to all values. This model included sex, predicted rank, and their interaction as fixed effects, and group identity as a random effect. Predicted rank was determined based on the relative size measured by standard length (e.g. the largest fish was predicted to be rank 1, second largest was predicted to be rank 2, and smallest fish was predicted to be rank 3). We used a post-hoc paired sample t-test to evaluate differences identified by the GzLM.

Fish in our study rarely entered the shelters. Even fewer fish (18 of 117) in our study were observed entering both shelters, we did not further evaluate whether there was a preference for the "high quality" versus "low quality" shelter. We suspect lack of use of shelters was due to the fish being unfamiliar with them (McCallum et al., 2017). As fish in our study had not had previous opportunities to assess shelters, we evaluated the time they spent in *either* shelter. In order to test whether time spent in shelters varied depending on sex, predicted rank, or their interaction, we created a GzLM with a negative binomial distribution (as data was overdispersed) and log link which included sex, predicted rank, and their interaction as fixed effects, as well group identity as a covariate. The dependent variable in this model was minutes spent inside a shelter.

In order to assess whether aggression within dyads was influenced by characteristics of the interactants, we ran a similar Generalized Linear Mixed Model (GzLM) with the summed count of aggressive behaviors of each member of a given dyad as the dependent variable. As this value was overdispersed, this model utilized a negative binomial distribution with a log link. This model included sex, dyad (Predicted Rank 1 vs. Predicted Rank 2, Predicted Rank 1 vs. Predicted Rank 3, Predicted Rank 2 vs. Predicted Rank 3), the size difference of the members of the dyad ((SL larger fish – SL smaller fish)/SL larger fish), and the two-way interactions of these factors as fixed effects, and group identity as a random effect. As before, we used a post-hoc paired sample t-test to evaluate differences identified by the GzLM.

In order to test whether some dominance relationships were resolved faster than others, we divided our behavioural observations into

Table 1
Results of Generalized Linear Mixed Model (GzLM) with a Poisson distribution and log link testing dominance index as the dependent variable.

Source	F	df1	df2	Sig
Corrected Model	97.737	5	111	< 0.001
Sex	0.35	1	111	0.556
Predicted Rank	219.508	2	111	< 0.001
Sex*Predicted Rank	2.91	2	111	0.059

four 15 min sections (0:00-15:00, 15:01-30:00, 30:01-45:00, 45:01-60:00). For each of these segments, we calculated dominance index scores for each individual and used these as the dependent variable in a GzLM with a normal distribution and log link. This model included Time, Sex, Predicted Rank, and the two-way interaction of each of these factors as fixed effects, and group identity as a random effect.

All statistical analyses were performing using SPSS version 25.0

2. Results

Size predicted the dominance index score for fish in our groups. The largest fish (which was predicted to be socially dominant) had the highest score, followed by the second largest, which was followed by the smallest fish (Predicted Rank 1 vs. Predicted Rank 2: $t_{38} = 5.019$, $p < 0.001$; Predicted Rank 1 vs. Predicted Rank 3: $t_{38} = 7.262$, $p < 0.001$; Predicted Rank 2 vs. Predicted Rank 3: $t_{38} = 2.244$, $p = 0.031$; see Table 1, Fig. 1). Sex, and the interaction of sex and predicted rank did not predict dominance index score. Predicted rank, sex, and their interaction did not predict the number of minutes a fish were identified as inside shelters (GzLM: Sex:$F_{1,111} = 0.003$, $p = 0.957$, Predicted rank: $F_{2,111} = 0.040$, $p = 0.961$, Sex*Predicted Rank: $F_{2,111} = 2.357$, $p = 0.099$).

There were significantly more aggressive interactions between the largest and second largest fish in each group than between either of the other two dyads ([Predicted Rank 1 vs. Predicted Rank 2] vs. [Predicted Rank 1 vs. Predicted Rank 3]: $t_{64.548} = 2.861$, $p = 0.006$; [Predicted Rank 1 vs. Predicted Rank 2] vs. [Predicted Rank 2 vs. Predicted Rank 3]: $t_{56.302} = 4.611$, $p < 0.001$; [Predicted Rank 1 vs. Predicted Rank 3] vs. [Predicted Rank 2 vs. Predicted Rank 3]: $t_{72.283} = 2.178$, $p = 0.033$; Table 2, Fig. 2). There were significantly fewer aggressive behaviors

Table 2
Results of Generalized Linear Mixed Model (GzLM) with a negative binomial distribution and log link testing summed aggression by both members of the dyad as the dependent variable.

| Source	F	df1	df2	Sig.
Corrected Model	2.775	9	107	0.006
Sex	0.01	1	107	0.922
Dyad	3.152	2	107	0.047
Size difference	0.012	1	107	0.914
Sex*Size difference	0.145	1	107	0.704
Dyad*Size difference	0.029	2	107	0.971
Sex*Dyad	0.387	2	107	0.68

between the second and third ranked fish in each group than between any of the other dyads (Table 2, Fig. 2). Size differences between the members of the dyad (Fig. 3), the sex of the members of the dyad, and the two-way interactions between each of these effects did not predict the summed count of aggressive behaviours within the dyad.

There was no impact of time on the dominance index score of group members, nor could any variation between each of the 15 min segments be explained by the interaction of segment (Time) or the sex or predicted rank of the fish (Table 3, Fig. 4). As in our first model, we found that the predicted rank of a fish predicted its dominance index score (Table 3, Fig. 4).

3. Discussion

We identified clear differences in dominance status between groups of three same-sex round goby. These differences were associated with the size of the individuals in each group, with larger individuals having higher dominance index scores. These dominance relationships were consistent throughout the observation period. Sex had no significant effect on differences in dominance relationships or the interactions through which they were established. While individuals in our groups varied in how different in size they were from their tank mates, this variation was not associated with variation in aggression within these dyads.

Size-based dominance hierarchies are widespread throughout social animal groups. In fish, there are many examples of size-based dominance hierarchies forming across species with drastically different
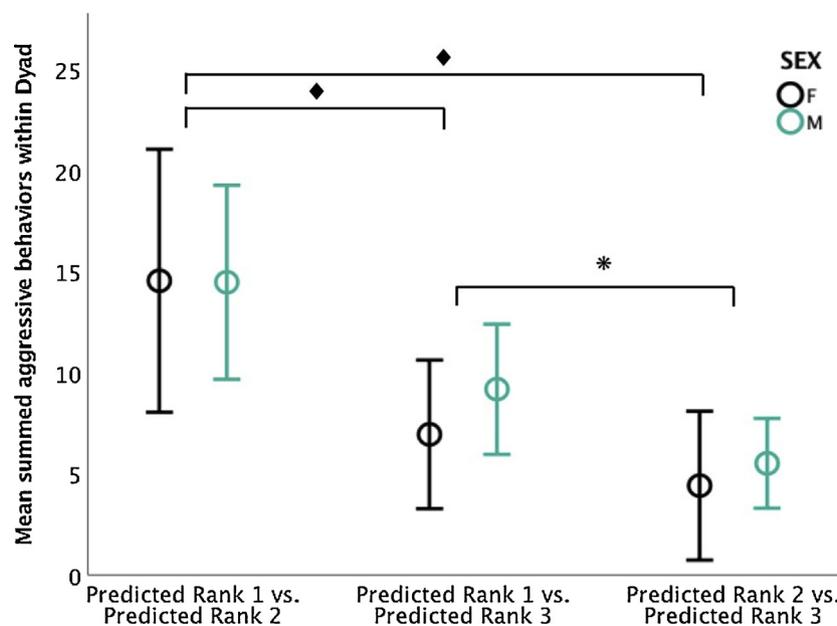
Fig. 1. Mean Dominance Index scores of goby based on predicted rank (larger fish were predicted to hold higher rank). Dominance Index was calculated as [Σ agg. beh. performed - Σ sub. beh. performed]. Error bars represent 95% CI. ◆ indicates $p < 0.001$, ✱ indicates $p < 0.05$ in post-hoc paired samples t-tests.
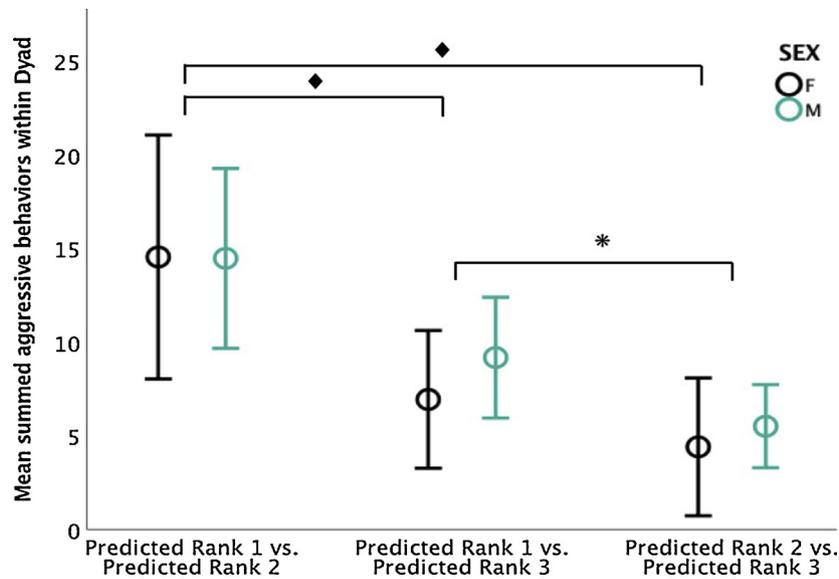
Fig. 2. Mean summed aggressive behaviors performed by both individuals in the dyad during 60 min observation period. Error bars represent 95% CI. ♦ indicates $p < 0.001$, ✱ indicates $p < 0.05$ in post-hoc paired samples t-tests.
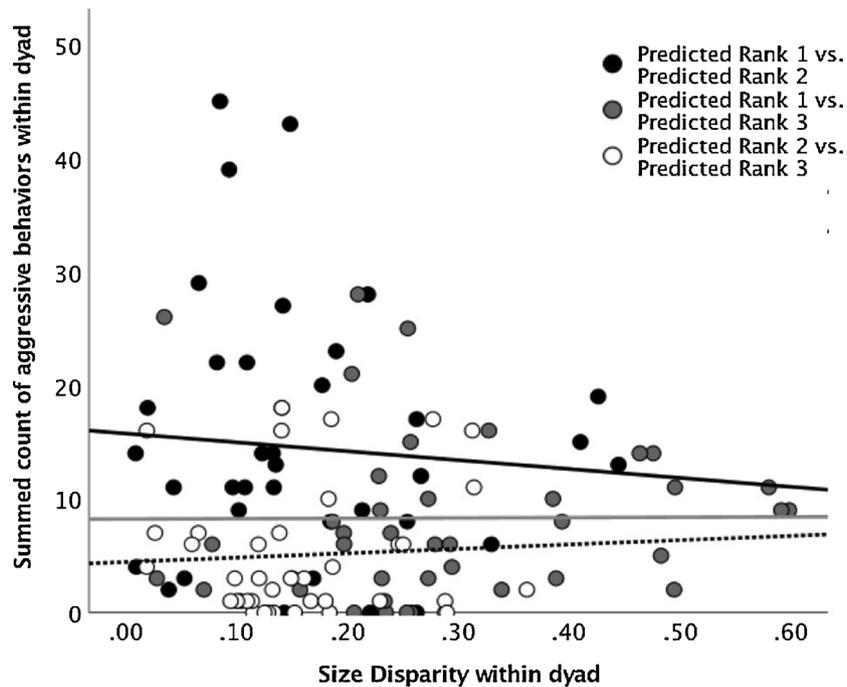

Fig. 3. Mean summed aggressive behaviors performed by both individuals in the dyad during 60 min observation period versus size disparity (standard length, SL) within the dyad. Size disparity calculated as [(SL of large fish − SL of small fish) / SL of large fish].

Table 3
Results of Generalized Linear Mixed Model (GzLM) with a normal distribution and identity link testing dominance index score (for each 15 min quarter of the observation) as the dependent variable.

Source	F	df1	df2	Sig.
Corrected Model	14.917	17	449	< 0.001
Sex	0.115	1	449	0.735
Time	0.05	3	449	0.985
Predicted Rank	110.818	2	449	< 0.001
Sex*Predicted Rank	1.377	2	449	0.253
Sex*Time	0.229	3	449	0.876
Time*Predicted Rank	0.874	8	449	0.514

social systems. In group living species such as many cichlids, damselfish, and goby species, dominance relationships have marked consequences for group membership, behavior within the group (Dey et al., 2013), reproductive opportunities (Hellmann et al., 2015), and even growth rates of group members (Buston, 2003; Heg et al., 2004; Wong et al., 2008). In less social fish species that form aggregations or simply compete with conspecifics, size is still an important determinant of which individuals are able to access food, shelter, or mates. Round goby likely fall into this latter category; individuals compete for access to shelter, and males compete for shelters, which they use to attract mates and defend young. In spite of this additional motivation to acquire greater access to resources such as shelter, we did not detect any differences in aggressive behaviors between males and females.

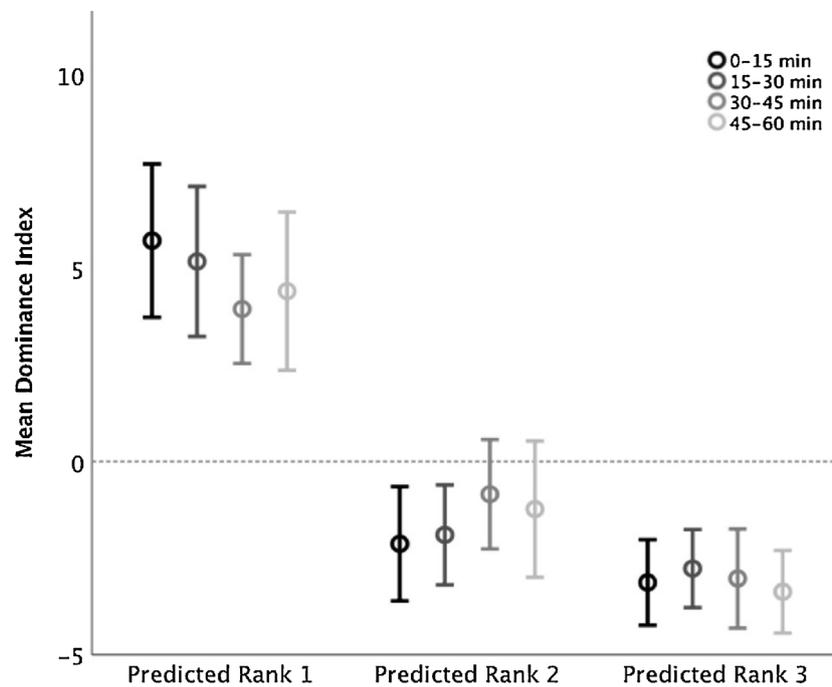Goby in our study were from an established invasive population

Fig. 4. Mean Dominance Index scores based on predicted rank; broken down into 15 min intervals. We identified the same differences based on predicted rank described in Fig. 1 and Table 1, but no effect of time. Error bars represent 95% CI.

with an extremely high density (nearly 7 fish per square meter in rocky habitats in western Lake Erie, Johnson et al., 2005). It is possible that in other populations, which did not evolve or develop at such high densities, fish could behave differently. Rubenstein (1981) found that depending on the density of pygmy sunfish, *Elassoma zonata,* males only established territories when the source of food was predictable or at higher densities. Magurran and Seghers (1991) found that populations of guppy, *Poecilia reticulata*, with an evolutionary history of high predation risk were more likely to aggregate into dense groups and performed fewer aggressive behaviours than individuals from populations accustomed to lower predation risk. Round goby in their native habitat, or along the "invasion front" likely live at lower population densities, and exhibit different patterns of dominance relationships. Groen et al. (2012) found that round goby from an invasion front won staged contests against individuals from an established invasive population. They attributed much of this to size asymmetries. Brandner et al. (2013) also found that growth and size was an important determinant of competitive ability along the invasion front in a population of round goby in the Danube river.

We did not identify any change in dominance relationships among the three goby over the course of our hour observation. It is possible that size differences were obvious enough that individuals had assessed one another and dominance relationships were established more or less immediately. In our observations, it was relatively rare for both individuals in a dyad to behave aggressively towards one another; generally, one individual was the aggressor throughout the observation, while the other responded to each aggressive behavior with a submissive or avoidance behaviour. In a more natural scenario, we would predict that aggressive interactions would eventually decline, either as a result of losers moving elsewhere (Fero and Moore, 2008) or because the dominance relationships had been settled and overt aggressive behaviors were no longer necessary (Berdoy et al., 1995). If this latter possibility is the case, our fish may not have been housed together long enough to allow the dominance relationships to shift. In order to test this possibility, future studies should examine changes within groups over days, weeks, or even the lifetime of the organisms.

Observer effects convey important information to individuals in social settings. Individuals may gain insights into the abilities of

potential competitors, and may in turn respond to these individuals accordingly (Earley and Dugatkin, 2002; McGregor, 2005). In some cases, third-party observers are predicted to capitalize on the losses of other individuals and in turn enhance their own status (Johnstone, 2001; McGregor, 2005). The largest members of our groups were involved in most aggressive interactions within groups. Summed counts of aggressive behaviors between the largest fish and the second, and third, respectively had the most and second most aggressive interactions of the three dyads in our groups. It is possible that smaller individuals benefited from observing interactions between the largest fish and other group members to inform their own behavioural decisions. If so, this would indicate that dominance relationships in more complex groups are established from the top down, either through initial assessment of conspecifics, direct aggressive interactions, or through indirect experience via observer effects. While we did not explicitly test this hypothesis, it would be possible to investigate how dominance hierarchies differ in groups of three (or more) members if individuals are added sequentially, and these newcomers do (or don't) have information about the competitive ability of other group members.

Round goby are an extremely successful invasive in the Laurentian Great Lakes (Kornis et al., 2012). Aggression has been suggested to be an important factor in the success of goby living along their invasion front (Groen et al., 2012), and is also influenced by exposure to contaminants (Sopinka et al., 2010). Additionally, the degree of sociality individual fish display also has important consequences along goby invasion fronts (Thorlacius and Brodin, 2018). Gaining deeper insights into the role of size, sociality, and aggression in the establishment of dominance relationships in this species is valuable for understanding the distribution of fish in habitats where they are already established, as well as for assessing their success along invasion fronts as they displace native species (Bergstrom and Mensinger, 2009).

Dominance relationships are widespread, and have important consequences for the behavior, survival, and fitness of individuals. We found that size has important consequences for the aggressive interactions between group members, as well as the dominance relationships that emerge from those aggressive interactions. In nature, dominance relationships are much more complex than dyadic conflict between opponents in staged encounters. Increasing the complexity with which

we evaluate dominance relationships will provide deeper insights into how dominance works in natural groups, and will allow us to better understand the consequences of dominance status for individuals, and its utility for populations and species. Our study takes a step towards this aspiration by investigating how dominance relationships form in complex social environments, and reinforcing the importance of size in resolving these relationships.

Acknowledgments

References

Archie, E.A., Moss, C.J., Alberts, S.C., 2006. The ties that bind: genetic relatedness predicts the fission and fusion of social groups in wild African elephants. Proc. R. Soc. B 273, 513–522.

Aubin-Horth, N., Desjardins, J.K., Martei, Y.M., Balshine, S., Hofmann, H.A., 2007. Masculinized dominant females in a cooperatively breeding species. Mol. Ecol. 16, 1349–1358.

Bayly, K.L., Evans, C.S., Taylor, A., 2006. Measuring social structure: a comparison of eight dominance indices. Behav. Process. 73, 1–12.

Beaugrand, J.P., Goulet, C., Payette, D., 1991. Outcome of dyadic conflict in male green swordtail fish, *Xiphophorus helleri*: effects of body size and prior dominance. Anim. Behav. 41, 417–424.

Berdoy, M., Smith, P., MacDonald, D.W., 1995. Stability of social status of wild rats: age and the role of settled dominance. Behaviour 132, 193–212.

Bergstrom, M.A., Mensinger, A.F., 2009. Interspecific resource competition between the invasive round goby and three native species: logperch, slimy sculpin, and spoonhead sculpin. Trans. Am. Fish. Soc. 138, 1009–1017.

Brandner, J., Cerwenda, A.F., Schliewen, U.K., Geist, J., 2013. Bigger is better: characteristics of round gobies forming an invasion front in the Danube River. Plos One 8, e73036.

Buston, P., 2003. Forcible eviction and the prevention of recruitment in the clown anemonefish. Behav. Ecol. 14, 576–582.

Chase, I.D., 1982. Dynamics of hierarchy formation: the sequential development of dominance relationships. Behaviour 80, 218–239.

Chase, I.D., Bartolomeo, C., Dugatkin, L.A., 1994. Aggressive interactions and intercontest interval: how long do winners keep winning? Anim. Behav. 48, 393–400.

Dewsbury, D.A., 1982. Dominance rank, copulatory behavior, and differential reproduction. Quart. Rev. Biol. 57, 135–139.

Dey, C.J., Reddon, A.R., O'Connor, C.M., Balshine, S., 2013. Network structure is related to social conflict in a cooperatively breeding fish. Anim. Behav. 85, 395–402.

Dugatkin, L.A., Druen, M., 2004. The social implications of winner and loser effects. Proc. R. Soc. B 271, S488–S489.

Earley, R.L., Dugatkin, L.A., 2002. Eavesdropping on visual cues in green swordtail (Xiphophorus helleri) fights: a case for networking. Proc. R. Soc. B 269, 943–952.

Engh, A.L., Siebert, E.R., Greenberg, D.A., Holekamp, K.E., 2005. Patterns of alliance formation and postconflict aggression indicate spotted hyaenas recognize third-party relationships. Anim. Behav. 69, 209–217.

Fero, K., Moore, P.A., 2008. Social spacing of crayfish in natural habitats: what role does dominance play? Behav. Ecol. Sociobiol. 62, 1119–1125.

Gherardi, F., 2006. Fighting behavior in hermit crabs: the combined effect of resource-holding potential and resource value in Pagarus longicarpus. Behav. Ecol. Sociobiol. 59, 500–510.

Gherardi, F., Daniels, W.H., 2003. Dominance hierarchies and status recognition in the crayfish Procambarus acutus acutus. Can. J. Zool. 81, 1269–1281.

Grant, J.W.A., 1997. In: Godin, J.G.J. (Ed.), Territoriality. In Behavioural Ecology of Teleost Fishes. Oxford University Press, pp. 81–103.

Groen, M., Sopinka, N.M., Marentette, J.R., Reddon, A.R., Brownscombe, J.W., Fox, M.G., Marsh-Rollo, S.E., Balshine, S., 2012. Is there a role for aggression in round goby invasion fronts? Behaviour 149, 685–703.

Heg, D., Bender, N., Hamilton, I., 2004. Strategic growth decisions in helper cichlids. Proc. R. Soc. B 271, S505–S508.

Hellmann, J.K., Ligocki, I.Y., O'Connor, C.M., Reddon, A.R., Garvy, K.A., Marsh-Rollo, S.E., Gibbs, H.L., Balshine, S., Hamilton, I.M., 2015. Reproductive sharing in relation to group and colony-level attributes in a cooperatively breeding fish. Proc. R. Soc. B 282, 0954 2015.

Holekamp, K.E., Smale, L., 1991. Dominance acquisition during mammalian social development: the "inheritance" of maternal rank. Am. Zool. 31, 306–317.

Hsu, Y., Wolf, L.L., 1999. The winner and loser effect: integrating multiple experiences. Anim. Behav. 57, 903–910.

Hsu, Y., Earley, R.L., Wolf, L.L., 2006. Modulation of aggressive behaviour by fighting experience: mechanisms and contest outcomes. Biol. Rev. 81, 33–74.

Hughes, C.R., Strassmann, J.E., 1988. Age is more important than size in determining dominance among workers in the primitively eusocial wasp, Polistes instabilis. Behaviour 107, 1–14.

Johnson, T.B., Allen, M., Corkum, L.D., Lee, V.A., 2005. Comparison of methods needed to estimate population size of round gobies (Neogobius melanostomus) in Western Lake Erie. J. Great Lakes Res. 31, 78–86.

Johnstone, R.A., 2001. Eavesdropping and animal conflict. PNAS 98, 9177–9180.

Kaufmann, J.H., 1983. On the definitions and functions of dominance and territoriality. Biol. Rev. 58, 1–20.

Kornis, M.S., Mercado-Silva, N., Vander Zanden, M.J., 2012. Twenty years of invasion: a review of round goby Neogobius melanostomus biology, spread and ecological implications. J. Fish. Biol. 80, 235–285.

Krause, J., James, R., Franks, D.W., Croft, D.P., 2015. Animal Social Networks. Oxford University Press.

Lindström, K., 1991. Effects of resource distribution on sexual selection and the cost of reproduction in sandgobies. Am. Nat. 158, 64–74.

Magurran, A.E., Seghers, B.H., 1991. Variation in schooling and aggression amongst guppy (Poecilia reticulata) populations in Trinidad. Behaviour 118, 214–234.

Martin, F., Beaugrand, J.P., Laguë, 1997. The role of hen's weight and recent experience on dyadic conflict outcome. Behav. Proc. 41, 139–150.

McCallum, E.S., Gulas, S.T., Balshine, S., 2017. Accurate resource assessment requires experience in a territorial fish. Anim. Behav. 123, 249–257.

McGregor, P.K., 2005. Animal Communication Networks. Cambridge University Press.

Øverli, Ø, Harris, C.A., Winberg, S., 1999. Short-term effects of fights for social dominance and the establishment of dominant-subordinate relationships in brain monoamines and cortisol in rainbow trout. Brain Behav. Evol. 54, 263–275.

Peake, T.M., Terry, A.M.R., McGregor, P.K., Dabelsteen, T., 2002. Do great tits assess rivals by combining direct experience with information gathered by eavesdropping? Proc. R. Soc. Lond. B 269, 1925–1929.

Pusey, A., Williams, J., Goodall, J., 1997. The influence of dominance rank on the reproductive success of female chimpanzees. Science 277, 828–831.

Reddon, A.R., Voisin, M.R., Menon, N., Marsh-Rollo, S.E., Wong, M.Y., Balshine, S., 2011. Rules of engagement for resource contests in a social fish. Anim. Behav. 82, 93–99.

Rubenstein, D.I., 1981. Combat and communication in the Everglades pygmy sunfish. Anim. Behav. 29, 249–258.

Rutberg, A.T., 1983. Factors influencing dominance status in American Bison cows (Bison Bison). Zeitschrift für Tierphychologie. 63, 206–212.

Schuett, G.W., 1996. Fighting dynamics of male copperheads, Agkistrodon contortix (Serpentes, Viperidae): stress-induced inhibition of sexual behaviors in losers. Zoo Biol. 15, 209–221.

Silk, M.J., Croft, D.P., Delahay, R.J., Hodgson, D.J., Boots, M., Weber, N., McDonald, R.A., 2017. Using social network measures in wildlife disease ecology, epidemiology, and management. BioScience 67, 245–257.

Sopinka, N.M., Marentette, J.R., Balshine, S., 2010. Impact of contaminant exposure on resource contests in an invasive fish. Behav. Ecol. Sociobiol. 64, 1947–1958.

Thorlacius, M., Brodin, T., 2018. Investigating large-scale invasion patterns using-small scale invasion successions – phenotypic differentiation of the invasive round goby (Neogobius melanostomus) at invasion fronts. Limnol. Oceanogr. 63, 702–713.

Wong, M.Y.L., Munday, P.L., Buston, P.M., Jones, G.P., 2008. Fasting or feasting in a fish social hierarchy. Curr. Biol. 18, R372–R373.