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Aerobic scope predicts dominance during early life in a tropical damselfish

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Summary

1. A range of physiological traits are linked with aggression and dominance within social hierarchies, but the role of individual aerobic capacity in facilitating aggression has seldom been studied. Further, links previously observed between an individual's metabolic rate and aggression level may be context dependent and modulated by factors such as social stress and fcompetitor familiarity.

2. We examined these issues in juvenile Ambon damselfish, *Pomacentrus amboinensis*, which display intraspecific competition for territories during settlement on coral reefs.

3. Individuals were measured for routine metabolic rate, aerobic scope (AS) and anaerobic capacity using intermittent-flow respirometry before dyadic dominance contests. Post-contest, fish were measured for metabolic rate in isolation and while interacting with their previous competitor or a stranger in adjacent transparent respirometers.

4. In arena contests, AS was correlated with aggression and dominance, while routine metabolic rate and anaerobic capacity were not related to dominance. Post-contest, subordinates showed a rise in metabolic rate and decrease in available AS, presumably due to social stress. Dominants increased metabolic rate in the presence of a previous competitor, possibly due to the stresses of hierarchy maintenance.

5. Metabolic rate during aggressive interactions did not approach that measured during exhaustive exercise, suggesting individuals do not fully utilise their AS during aggression. A greater AS may, however, allow faster post-contest recovery.

6. These results demonstrate a link between AS and dominance during intraspecific competition for territory. Selection on AS could therefore follow, either indirectly through correlations with other traits influencing resource-holding potential, or directly if AS carries benefits important for territory acquisition or holding, such as an enhanced capacity to cope with socially induced stress.

Key-words: competitor recognition, conflict, dear enemy effect, ecophysiology, fish, intraspecific competition, metabolic rate, territoriality

Introduction

Variation in aggression among individuals within a number of animal species can determine status within social hierarchies, which in turn affects life-history strategies, reproductive success and survival (Briffa & Sneddon 2007; Huntingford, Tamilselvan & Jenjan 2012; Majolo *et al.* 2012). While traits such as body size and aggression strongly influence dominance, detailed knowledge of the physiological traits underpinning variation in aggressive behaviours remains elusive. Despite positive correlations between resting metabolic rate and aggression among

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*Correspondence author. E-mail: shaun.killen@glasgow.ac.uk individuals (Biro & Stamps 2010), the direction of this causal association, if one exists, is ambiguous and likely variable depending on context. For example, it is uncertain whether a higher resting metabolic rate and a corresponding need to acquire resources drives aggression during intraspecific competition (Metcalfe, Taylor & Thorpe 1995), or whether the outcome of prior social interactions influences metabolic rate and subsequent competitive ability (Dijkstra *et al*. 2012). Further complicating associations between aggression and metabolic traits are the effects of social stress. Subordinate individuals can show an increase in metabolic rate due to the stress of harassment from conspecifics (Senar *et al*. 2000; Sloman *et al*. 2000), while dominant individuals can experience stress associated with maintaining social hierarchies or territory defence (Røskaft *et al*. 1986; Castro *et al*. 2006).

Although several studies have documented large energetic costs of physical activity during aggressive encounters (Briffa & Sneddon 2007), the effects of individual aerobic capacity on aggression have been mostly overlooked. Aerobic scope (AS) – the difference between an animal's minimal and maximal rates of aerobic metabolism (Fry 1971; Pörtner & Farrell 2008) – has recently been proposed as an important trait influencing behaviours and ecological interactions (Killen *et al*. 2007; Pörtner & Farrell 2008), but to date there have been few attempts to directly examine the importance of AS in the context of behavioural ecology. AS could, however, facilitate aggression by allowing an animal to perform increased aerobic activity as well as recover faster from intense anaerobic exercise that can occur during aggressive interactions (Briffa & Sneddon 2007). An additional benefit of a large AS might be that any effects of social stress on metabolic rate could have a relatively small effect on the proportion of remaining AS available for other physiological tasks (e.g. growth, activity, digestion) following an aggressive encounter.

The stress associated with territory maintenance can be modulated by the degree of familiarity with neighbours or previous competitors. In numerous taxa, it has been observed that territory establishment is followed by decreased aggression between familiar neighbours [the 'dear enemy' effect (Ydenberg, Giraldeau & Falls 1988; Skierczynski, Czarnecka & Osiejuk 2007; Briefer, Rybak & Aubin 2010)], and a higher amount of aggression directed towards strangers (i.e. individuals not previously encountered). One hypothesis is that neighbours opt to reduce the time and energy expended on rivalries that have already been settled (Temeles 1994; Müller & Manser 2007). However, the energetic savings actually achieved through neighbour/stranger discrimination have not been examined. In addition, some species appear to display increased aggression towards neighbours as compared to strangers (Müller & Manser 2007; Schradin, Schneider & Lindholm 2010). This may occur when neighbours present more of a threat than strangers, but the situations in which this occurs and the implications for energy expenditure and AS usage are unknown. More information on the metabolic consequences of distinguishing between neighbours and strangers would be useful for understanding the energetic basis of trade-offs associated with resource-holding and territorial defence.

In many tropical damselfishes, competition for territory is intense during the early juvenile stage immediately after young fish migrate from the pelagic zone to coral reef habitat for settlement. It has been estimated that over 55% of juveniles are preyed upon within several days of arriving on the reef (Almany & Webster 2006). In fact, predation can be so intense that individuals may prioritise safety over food availability when selecting territories (McCormick 2009). Dominant individuals take optimal sites with shelter and refuge from predators being the primary resource being contested during settlement (McCormick, Watson & Munday 2013). The settlement stage therefore represents a selective bottleneck in which aggression and dominance could influence which phenotypes gain an advantage. It is also noteworthy that adjacent territories among conspecifics can be within close proximity and therefore individuals are likely to repeatedly encounter the same rival. Conspecific recognition has been demonstrated in some adult reef fishes (Thresher, Colin & Bell 1989; Siebeck *et al*. 2010) and could mediate the amount of aggression displayed towards potential threats to territoriality and dominance (Poulos & McCormick 2014). However, the metabolic response to encountering familiar and strange individuals has not been investigated. Changes in metabolic rate in response to intruders should be especially important during the early life stages of fish because they already have an elevated metabolism and constrained AS during early ontogeny (Killen *et al*. 2007; Nilsson *et al*. 2007).

In this study, we investigated the relationships between metabolic phenotypes (i.e. metabolic rate and AS) and aggression during dyadic contests in settlement stage juveniles of the Ambon damselfish, *Pomacentrus amboinensis*. Specifically, we aimed to address the following questions: (i) Is aggression linked to metabolic rate or AS; (ii) How do dominance contests alter the metabolic rate of individuals; and (iii) Do individuals recognise and respond differently (behaviourally and metabolically) to previous opponents? Because predation as a selective force is extremely important during this life stage, any effects of metabolic traits on the ability to secure refuge or territory could play a major role in determining which phenotypes have a selective advantage.

Materials and methods

We examined the links between metabolic traits and aggression in juvenile damselfishes using, in order, the following procedures: (i) measuring precontest metabolic traits; (ii) observing dyadic dominance trials in an experimental arena (n = 72 individuals, making 36 pairs); (iii) measuring post-contest changes in metabolic rate in dominants and subordinates; and (iv) visually exposing individuals to either a stranger or previous competitor through transparent walls of adjacent respirometers and measuring the resulting behavioural and metabolic responses.

ANIMALS

Pomacentrus amboinensis (Pomacentridae) is a benthic damselfish that is a common member of the coral reef fish community in shallow waters (< 20 m depth) of the Indo-Pacific. They are a planktivore and habitat generalist at the study location. While they prefer to settle on live coral (McCormick, Moore & Munday 2010), juveniles and adults are found on the reef edge associated with a mixture of live, dead coral and sand (McCormick & Meekan 2007). Juveniles show high levels of aggression when they first settle that is positively correlated with survival in the field (McCormick & Meekan 2010).

Settlement-stage juveniles of *P. amboinensis* were collected using light traps moored overnight in open water on the western side of Lizard Island (14′40ºS, 145′28ºE), in the northern Great Barrier Reef, Australia. Fishes were sorted to species and kept for 3 days in flow-through aquaria at the Lizard Island Research Station supplied with local seawater at ambient temperatures (28–29 °C). Fish were fed *Artemia* nauplii until 20 h before the onset of experimental procedures. On the day before each fish was used in experiments, they were placed into individually labelled clip-seal bags, measured for length with callipers and then given a small tag with elastomer for later identification during contests in the experimental arena (Hoey & McComick 2006).

PRECONTEST METABOLIC RATE AND AEROBIC SCOPE

Metabolic rate was estimated for each individual before intraspecific contests by measuring oxygen uptake using intermittent-flow respirometry. To estimate maximal metabolic rate (MMR), fish were individually exercised to exhaustion by manual chasing in a small (20 cm diameter) container filled to a depth of 5 cm. Fish were considered exhausted when they would no longer respond to chasing by burst swimming (mean time of exhaustion = 80·88 ± 3·32 s). Fish were then immediately transferred to individual cylindrical glass respirometers with acrylic end-caps (total volume of chamber plus associated tubing = ~70 mL). The average time until transfer to the respirometers after exhaustion was 9·55 ± 0·32 s. This method elicits anaerobic exercise in individuals and maximal rates of oxygen uptake are measured during subsequent recovery (Reidy *et al.* 1995; Killen *et al.* 2007; Clark, Sandblom & Jutfelt 2013). Respirometers were immersed in a water bath supplied with flow-through water from a separate header tank at ambient temperatures (28·89 ± 0·17 °C mean daily temperature over the course of the study). Fish were left undisturbed in respirometers for the following 2·5 h. The spontaneous activity (number of movements during a 5 min period) of each individual within the chambers was quantified from video recordings taken from above the chambers at 0, 60 and 120 min of confinement within respirometers. Activity was minimised by placing a piece of black tape on the surface of the upper middle portion of each chamber; fish would use this area as shelter, thus discouraging them from moving in the respirometers. Opaque dividers were placed between adjacent respirometers to prevent visual contact between fish. Water flow through respirometers was driven by an external pump in the adjacent header tank set to alternatingly turn on (5 min) and off (15 min) throughout the measurement period. This allowed water oxygen content to be measured every 2 s for 15 min while the respirometer was in the closed state, after which the respirometer was flushed with aerated water for 5 min. An exception to this was the first 30 min following exhaustive exercise, during which time the flush pump remained off so that rates of oxygen uptake could be measured throughout the entire immediate recovery phase. Water mixing within each respirometer was achieved with a peristaltic pump that moved water through the chamber and round an external circuit of gas-impermeable tubing. Also located within the circuit for each respirometer was a flow-through cell that housed an oxygen-sensing optode attached to an oxygen sensor (Firesting 4-Channel oxygen metres; Pyroscience, Germany) and computer. Slopes were calculated from the plots of oxygen concentration versus time using linear least squares regression (LabChart v. 7.3.7 ADInstruments, Dunedin, New Zealand). These slopes were then converted to mass-specific rates of oxygen uptake (mg O_2 kg^{-1} h^{-1}) using standard equations (Claireaux & Lagardère 1999). After 2·5 h, the fish were placed into individual holding containers (700 mL) supplied with flow-through seawater and fed *Artemia* nauplii. To correct for background bacterial oxygen consumption, all respirometers were run empty at the beginning and end of each working day. Each morning all respirometers, flow-through cells and tubing were thoroughly cleansed with soap and hot water.

Routine metabolic rate (RMR) was estimated as the mean level of oxygen uptake during the final hour of respirometer confinement. For maximal metabolic rate (MMR), we calculated rates of oxygen uptake for each 3 min time interval throughout the first 30 min of recovery immediately following exhaustive exercise. We then used a three-parameter exponential function to determine the rate of oxygen uptake immediately following exhaustive exercise, estimated as the y-intercept of the plot of oxygen uptake versus time. This method for determining MMR was required for two reasons: (i) the first 1 min after transfer of fish to the respirometers was excluded from analyses so that adequate mixing within the chamber and external circuit could occur, providing accurate measures of water oxygen concentration; and (ii) the recovery of individuals after exercise was rapid (Fig. S1, Supporting information), and we aimed to estimate oxygen uptake as close to the cessation of exercise as possible. Intercept values were strongly and positively correlated with the maximum rates of oxygen uptake obtained throughout the measurement period (Pearson correlation, $r = 0{\cdot}743$, $P < 0{\cdot}0001$) but are reflective of oxygen uptake immediately following exhaustive exercise in each individual and therefore allow a more accurate estimation of AS.

Aerobic scope was calculated as the difference between MMR and RMR. AS in fishes is typically calculated as the difference between MMR and standard metabolic rate (SMR), the latter of which is determined using data collected over at least several hours (Killen *et al.* 2012; Clark, Sandblom & Jutfelt 2013). Damselfish at this life stage, however, are vulnerable to starvation (McLeod *et al.* 2013) and so our aim was minimise the time they spent in the respirometry chambers after fasting, especially given that they would subsequently be involved in a series of aggressive encounters over the study period. However, we feel that our measures of RMR closely match SMR for several reasons. Spontaneous activity within respirometers during the final hour of confinement was low (1·62 ± 0·24 movements min^{-1}), and it was not related to any metabolic trait, including RMR (general linear models, effect of activity, $P > 0{\cdot}05$). Pilot trials in which fish were left in respirometers for 8 h demonstrated that individuals recovered extremely quickly from exhaustive exercise and stabilised oxygen uptake within 90 min post-exercise. Identical results were observed for data used in the current study (Fig. S1). Therefore, our estimates of AS are likely to include the amount available for additional activity that could be used for foraging, territory defence, predator avoidance and other tasks.

Excess post-exercise oxygen consumption (EPOC) for each individual was estimated by calculating the area under the three-parameter exponential recovery function until the time at which fitted values were equal to individual RMR. EPOC represents the increase in oxygen consumption above resting levels occurring during recovery from a bout of exhaustive anaerobic exercise and represents the anaerobic capacity of an animal (Gastin 1994; Lee *et al.* 2003; Svendsen *et al.* 2010). The rate of recovery from exercise was assessed by measuring the time taken for each individual to recover 50% of its AS following exhaustive exercise (AS_{50}; Marras *et al.* 2010).

DOMINANCE CONTESTS

The following day fish were placed into a 50 × 25 cm experimental arena filled to a depth of 10 cm for dyadic dominance contests. Pairs of fish were size-matched to the nearest 0·1 cm total length ($n = 36$ pairs). Fish started at the same end of the arena but were separated by an opaque wall that ran lengthwise through the middle of the tank for 32 cm. At the opposite end of the arena from the starting point was a piece of live coral (approximately 7 cm diameter). To begin the trial, each fish was placed within a starting chamber which consisted of an upright PCV cylinder with a revolving door. After a 5 min acclimation period, the doors to the chambers were opened and the fish were free to emerge. Individuals could explore their portion of the arena but were prevented from reaching the coral refuge by a clear partition blocking that end of each fish's section of the arena. Competitors remained unaware of each other's presence within the arena at this time, but both could become knowledgeable of the location of the coral. After an additional 5 min, the clear partition was removed and the fish were free to approach the coral or interact with their competitor. The entire trial from the opening of the starting chambers to the end of the first 10 min of competitive interaction was recorded using a video camera mounted above the arena. From the videos, we quantified three types of behaviour: (i) displays, in which the fish would flare its fins or turn laterally towards its opponent; (ii) attacks, in which fish would bite or chase its opponent; and (iii) avoids, in which the fish would actively move away from a display or attack. Time spent closest to the coral was also quantified. An aggression score was calculated for each individual in which aggression = (attacks × 3) + displays – avoids (McCormick & Weaver 2012; McCormick, Watson & Munday 2013). In each competition, the fish with the highest aggression score was deemed to be dominant. After the period of recording fish were left together in the arena for an additional 50 min.

POST-CONTEST METABOLIC RATE AND CONSPECIFIC RECOGNITION

Following dominance trials fish were removed from the experimental arena and carefully transferred without air exposure to the respirometry chambers. Measurements of oxygen uptake then continued undisturbed for 2 h, with video recordings being taken at 0, 60 and 120 min after transfer for later analysis of spontaneous activity. Fish were then visually exposed to individuals in adjacent respirometers (0·5 cm between neighbouring chambers; chambers were 8·5 cm L × 3·2 cm W) by the removal of the one opaque partition on either side of the respirometer. In this manner fish were sequentially exposed to either: (i) their previous competitor from the dominance trial; or (ii) a fish that they had not encountered before (i.e. a stranger; size-matched within a 0·1 cm difference). Each exposure began 1 min prior to the initiation of oxygen uptake measurements, and lasted for an additional 15 min. As a control, some fish ($n = 18$) were exposed to an empty chamber. Exposure order was randomised with 10 min between exposures. All interactions between fish in adjacent respirometers were recorded by a video camera mounted above the chambers, and displays, attacks, avoids, and activity were later quantified as previously described, except in this case attacks did not include bites or chases because fish were unable to come into contact. Following these trials, fish were removed from chambers and measured for wet mass.

DATA AND STATISTICAL ANALYSES

Statistics were performed using SPSS v20.0 (SPSS Inc., Chicago, IL, USA and IBM, Armonk, NY, USA). The level of significance for all tests was $\alpha = 0{\cdot}05$. When required, normality, linearity and homogeneity of residuals were verified by inspection of residual-fit plots. Values in test are mean ± SEM.

Metabolic traits (i.e. RMR, MMR, AS, EPOC, AS_{50}), as measured before the pairwise dominance trials, were compared between dominant and subordinate fish using general linear models (GLMs). Status was used as a categorical variable and mean activity level in respirometers and mass were used as covariates. Behaviours (i.e. displays, avoids, aggression and time closest to coral) measured during the dyadic dominance trials were compared between dominant and subordinate individuals using linear mixed models (LMMs) with status as a categorical variable, RMR, MMR, AS and mass as covariates, and fish ID nested within pair as a random effect. The time taken to emerge from starting chamber at the beginning of the dyadic dominance trials was compared between dominant and subordinate fish using GLMs with status as a categorical variable and RMR, MMR, AS and mass as covariates. Among pairs, correlations between either the difference in RMR, MMR and AS between competitors and the difference in aggression observed were examined using Pearson correlations. The effect of the difference in RMR, MMR and AS on the total amount of aggression observed in contests was also examined using Pearson correlations.

Post-competition changes in metabolic rate were examined using LMMs, with the percentage change in metabolic rate (as compared to post-competition RMR) as the dependent variable, status as a categorical explanatory variable, time (measurement period) as a repeated variable, mass as a covariate and fish ID as a random effect nested within pair. The effects of exposures to either a stranger or prior competitor on metabolic rate and behaviour (aggression) were examined using LMMs with either the percentage change in metabolic rate (as compared to metabolic rate immediately prior to exposure) or aggression as the dependent variable, status as a categorical explanatory variable, opponent (i.e. stranger, neighbour, or control) as a repeated variable, mass as a covariate and fish ID as a random effect nested within pair.

Results

PRECONTEST METABOLIC RATE AND AEROBIC SCOPE

Fish that became dominant in pairwise contests had a higher MMR (Figs 1a and S1; GLM, effect of status, $F_{1,71} = 7{\cdot}089$, $P = 0{\cdot}010$) and AS (GLM, effect of status, $F_{1,71} = 8{\cdot}242$, $P = 0{\cdot}005$) when compared to subordinates. RMR measured precontest did not differ between dominant and subordinate individuals (GLM, effect of status, $P > 0{\cdot}05$). Dominant fish tended to have a higher EPOC as compared to subordinates but this difference was not statistically significant (dominants = 417·27 ± 4370 mg $O_2\ kg^{-1}$, subordinates = 325·87 ± 39·88 mg $O_2\ kg^{-1}$; GLM, effect of status, $F_{1,71} = 3{\cdot}15$, $P = 0{\cdot}08$). Both dominants and subordinates recovered from exercise quickly with no statistical difference between groups (dominants = 10·25 ± 1·37 min, subordinates = 12·33 ± 2·08 min; GLM, effect of status, $F_{1,71} = 0{\cdot}593$, $P = 0{\cdot}444$). However, AS_{50} was strongly correlated with EPOC (GLM, $F_{1,71} = 8{\cdot}70$, $P < 0{\cdot}001$), with fish having a higher anaerobic capacity and subsequent payback phase (i.e. a higher EPOC) taking longer to recover to

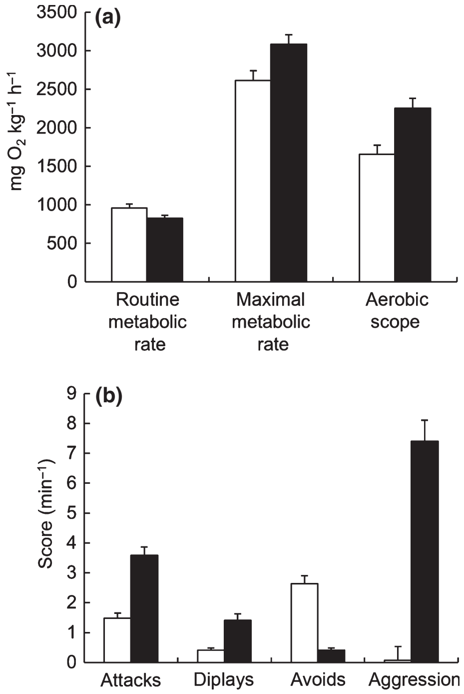

Fig. 1. Precontest metabolic traits and behaviour during contests for dominant and subordinate Ambon damselfish. (a) precontest metabolic traits; and (b) behaviours during dominance contests. Note that fish within each pair were designated as being either dominant or subordinate based on their overall aggression score. The intent of panel b is to therefore illustrate the overall magnitude of the differences in behaviour between dominant and subordinate individuals. Dark bars represent dominant individuals; open bars represent subordinates. Error bars represent standard error of the mean.

AS_{50}. To examine the main effect of social status on rate of recovery after exercise while correcting for variation in EPOC, an additional GLM for AS_{50} was run in which EPOC was included as a covariate. In this model, dominant individuals had a faster rate of recovery after exercise (GLM, effect of status, $F_{1,71} = 6{\cdot}292$, $P = 0{\cdot}015$). Across all individuals, fish with a higher AS recovered faster after exhaustive exercise (Pearson correlation between AS and AS_{50}: $r = -0{\cdot}416$, $P < 0{\cdot}001$).

DOMINANCE TRIALS

Dominant fish emerged sooner from the starting chamber (8·33 ± 2·03 s) when compared to subordinates (19·88 ± 6·10 s; GLM, effect of status, $F_{1,71} = 4{\cdot}017$, $P = 0{\cdot}049$). Overall, fish with a higher RMR also emerged from the starting chamber sooner (GLM, effect of RMR, $F_{1,71} = 10{\cdot}064$, $P = 0{\cdot}002$), while AS was not related to emergence time. When allowed to explore the entire arena, fish invariably displayed a strong attraction to the coral refuge. Upon noticing their competitor, individuals would always engage in an aggressive interaction almost immediately (see Video S1, Supporting information for an example interaction that was not scored as part of this study). Interactions tended to begin with displays and later escalated to attacks. Dominant individuals showed more displays (Fig. 1b; LMM, effect of status, $F_{1,38{\cdot}67} = 15{\cdot}68$, $P < 0{\cdot}001$) and attacks ($F_{1,36{\cdot}91} = 49{\cdot}236$, $P < 0{\cdot}001$), fewer avoids ($F_{1,68} = 50{\cdot}189$, $P = < 0{\cdot}001$) and a higher aggression score (though this is how dominance was defined; $F_{1,68} = 61{\cdot}004$, $P < 0{\cdot}001$). Dominant fish also spent a greater proportion of time closest to the coral refuge (LMM, effect of status, $F_{1,68} = 20{\cdot}037$, $P < 0{\cdot}001$). While dominants and subordinates showed large differences for each type of behaviour, subsequent analyses focus on aggression score because this is an integrative measure of the level of antagonism displayed by individuals.

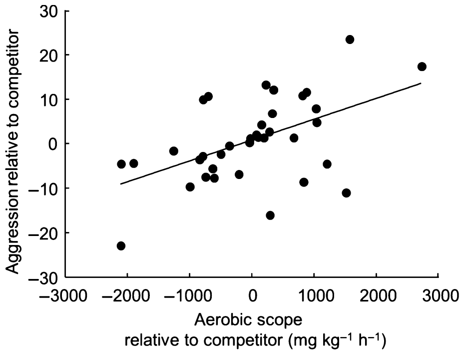

Fig. 2. Correlation between differences in aggression by individuals in dyadic contests and difference in aerobic scope ($y = (0{\cdot}0047{*}x) + 0{\cdot}8042$, $r^2 = 0{\cdot}267$, $P = 0{\cdot}001$). Each point represents one randomly selected individual from each pair used in the current study.

Neither RMR nor AS were associated with absolute aggression score of individuals in dominance trials (LMM, effects of RMR and AS, $P > 0{\cdot}05$). However, individuals with the highest AS became dominant in 28/36 pairs (77·8%), significantly higher than expected by chance (chi-square test, $\chi^2 = 11{\cdot}11$, $P < 0{\cdot}001$). The difference in AS observed between competitors was positively correlated with the difference in the amount of aggression displayed between competitors (Fig. 2; Pearson correlation, $r = 0{\cdot}517$, $P = 0{\cdot}001$), indicating that a greater the discrepancy between an individual and its competitor was related to more aggression displayed by the dominant individual. Individual RMR, or the difference in RMR between competitors, was not related to the outcome of contests or the amount of aggression displayed.

POST-CONTEST METABOLIC RATE AND CONSPECIFIC RECOGNITION

Following pairwise contests, subordinate individuals had a relative increase in metabolic rate compared to dominant individuals. The difference in metabolic rate between subordinates and dominants increased during the 2 h post-contest measurement period (Fig. 3; LMM, status x time interaction, $F_{1,192{\cdot}39} = 23{\cdot}823$, $P < 0{\cdot}001$). When compared to precontest metabolic rate, repeatability of metabolic rate across individuals was moderate (intraclass correlation coefficient = 0·324; Spearman correlation, $r = 0{\cdot}376$, $P = 0{\cdot}001$). The percentage change in metabolic rate (compared to RMR) was related to the difference in aggression an individual experienced relative to its neighbour during the dominance contest (Fig. S2, Supporting information; LMM with fish ID nested within pair as a random effect, $F_{1,59} = 5{\cdot}972$, $P = 0{\cdot}018$).

When exposed to either a stranger or their previous competitor while in the respirometry chambers, dominant fish showed a larger change in oxygen uptake as compared to subordinates (LMM, effect of social status, $F_{1,55{\cdot}49} = 7{\cdot}00$, $P = 0{\cdot}011$). However, both dominants and subordinates showed a greater increase in oxygen uptake when exposed to their prior competitor compared to a stranger (Fig. 4; LMM, effect of familiarity, $F_{2,32{\cdot}27} = 5{\cdot}624$, $P = 0{\cdot}008$). There was no interaction between status and competitor familiarity on the observed change in oxygen uptake (LMM status × familiarity interaction, $P > 0{\cdot}05$). Individuals that were dominant in the arena trials displayed more aggression during conspecific exposures within the respirometry chambers (LMM, effect of status, $F_{1,68{\cdot}971} = 5{\cdot}067$, $P = 0{\cdot}028$), regardless of whether they were being exposed to a stranger or a prior competitor (LMM, effect of exposure, $P > 0{\cdot}05$). However, the levels of activity or aggression displayed in the chambers were not linked to metabolic rate measured during interactions in the respirometry chambers (LMM, effects of activity and aggression, $P > 0{\cdot}05$).

Discussion

Our results demonstrate a complex array of associations between aggression and metabolic traits in juvenile damselfish as they compete for territory. While aggression and the probability of becoming dominant are linked with individual AS, the outcomes of such interactions induce changes in the metabolic rate of subordinate individuals, at least over the short-term, thus causing corresponding changes in the available AS for other physiological tasks. Interestingly, the effects of competitive interactions on metabolic rate are modulated by the degree of familiarity between an individual and its competitor. Contrary to predictions, individuals did not display less aggression towards prior competitors. Instead, individuals displayed similar levels of aggression to strangers and familiar fish, but showed a stronger metabolic response to the presence of a previous competitor. These results suggest that in the wild, individuals with a higher AS may be better able to obtain safer territories and potentially gain a selective advantage.

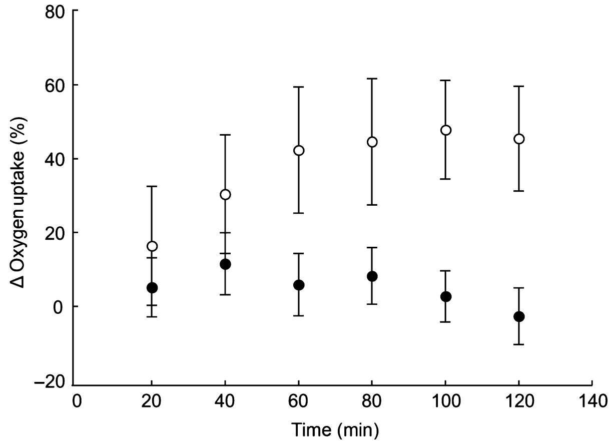

Fig. 3. Changes in oxygen uptake rate, relative to precontest RMR, following dyadic dominance contests. Dark circles represent individuals that were dominant; open circles represent individuals that were subordinate. Error bars represent standard error of the mean.

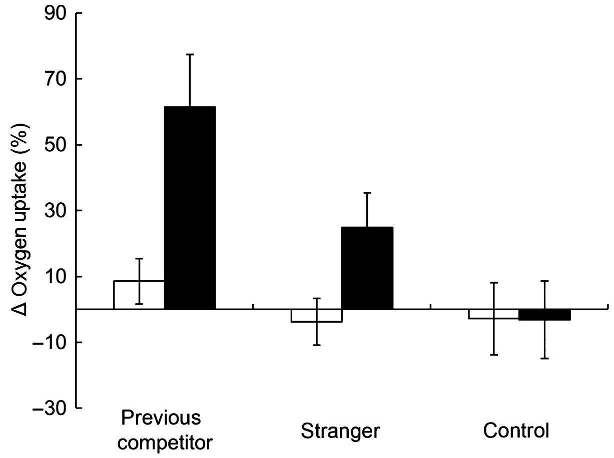

Fig. 4. Oxygen uptake, relative to that 2 h post dyadic contest, in individuals exposed to a prior competitor or stranger. Control individuals were exposed to an empty chamber without another fish. Dark bars represent individuals that were dominant in dyadic arena contests; open bars represent individuals that were subordinate. Error bars represent standard error of the mean.

IS COMPETITIVE OUTCOME LINKED WITH METABOLIC RATE OR AEROBIC SCOPE?

Aerobic scope was not associated with the absolute amount of aggression displayed by individuals. Within pairs, however, individuals with the highest AS were dominant most often. This link between AS and dominance is likely related to the physical activity displayed during these interactions, which may be facilitated by a higher AS. Further, while all fish recovered extremely quickly after exhaustive exercise, dominant individuals recovered faster than subordinates (after controlling for variation in EPOC), and fish with a higher AS were able to recover from exhaustive exercise faster (Marras *et al.* 2010). Thus, an increased AS could allow dominant individuals to resume activity sooner after an altercation and be better prepared for subsequent foraging bouts or predator evasion (Briffa & Sneddon 2007). It is also possible that AS and dominance are correlated with a third, unmeasured variable that signals high quality and encourages those with a lower AS to respond with submission. This is supported by the observation that, during competitive interactions within the respirometry chambers, metabolic rates of individuals generally remained below their MMR, suggesting that a high AS is not necessarily required for an individual to perform physical activity during an antagonistic encounter. Similarly, it has previously been shown that maximal sprint speed in lizards is positively correlated with dominance, despite the fact that these speeds are never achieved in a contest scenario (Garland, Hankins & Huey 1990).

It is noteworthy that there was no relationship between RMR and aggression or dominance among juvenile damselfish despite indices of resting metabolic rate being linked to aggression in numerous other taxa, including several fishes (Metcalfe, Taylor & Thorpe 1995; Biro & Stamps 2010). In most of these instances, however, the priority for territory selection is food availability. The available evidence, however, suggest that the juveniles of several damselfish species prioritise safety (McCormick 2012; McCormick & Weaver 2012). When food is abundant, phenotypes with a high metabolic rate should have an advantage in terms of maximising growth (Burton *et al.* 2011). For some damselfishes, including Ambon damselfish, dominant juveniles in the wild occupy positions at the base of the reef where there is more protection but less planktonic food (McCormick 2012; McCormick & Weaver 2012). Therefore, a high baseline metabolic rate for dominant fish in these microhabitats could actually be a disadvantage because they would have to satisfy relatively high energetic requirements while having fewer foraging opportunities.

HOW DO DOMINANCE CONTESTS ALTER METABOLIC RATE?

Subordinate individuals showed an increased metabolic rate post-contest but dominants showed no change. Activity level within respirometry chambers was the same before and after the arena dominance contests (LMM, effect of measurement period, $P < 0{\cdot}05$), suggesting the increase in oxygen uptake stemmed from social stress resulting from the preceding aggressive interaction. Such effects on subordinate individuals have previously been documented in fish and other taxa as a result of intraspecific conflict (Senar *et al.* 2000; Sloman *et al.* 2000). This increase in metabolic rate could represent an energetic cost for subordinates, in addition to the potential costs of subordination associated with endocrine effects on growth rate, immune function, and overall health (Sloman & Armstrong 2002; Sapolsky 2005). Beyond increased energetic expenditure, the effect of a socially induced stress response may be important if it comprises a significant portion of the AS of an animal and thus constrains the capacity to simultaneously perform oxygen-consuming physiological tasks. For example, the mean maximal increase of oxygen uptake during the post-contest measurement period in subordinates was $300{\cdot}33 \pm 77{\cdot}6$ mg kg^{-1} h^{-1}. This correspondingly decreased the available AS of subordinates by an average of 17·39%. There was variability around this response, however, with several individuals (7/36 subordinates) decreasing their available AS by a maximum of 40–95% as a result of post-contest increases in metabolic rate. This reduction in AS could constrain physiological function, especially if accompanied by thermal stress or increased water velocity, potentially leading to increased risk of mortality (Priede 1985).

Upon arriving on the reef, individuals with a greater AS may have a selective advantage if they are better able to obtain territory, process food, cope with environmental stressors and avoid predation. It is unclear, however, whether AS would be a trait under direct or correlated selection in this context. Firstly, if dominance and AS are both correlated with some other, unmeasured trait influencing territory acquisition, then the association between AS and resource-holding potential would be indirect, with AS under correlated selection with other traits. Still, AS could be under direct selection if it carries benefits, such as increased recovery rate after conflicts or a greater capacity to accommodate social stress with minimal impact on aerobic physiological tasks. However, if the outcomes of competitive interactions shuffle the rankings of surplus AS among subordinate individuals, which have not yet claimed territories, then the short-term repeatability of available AS may be diminished to the point where selection on intrinsic AS could be reduced or unstable (Dohm 2002). Similar to the study of Sloman *et al.* (2000), the magnitude of change in the metabolic rate of individuals post-contest was related to the degree of aggression received during dominance trials. Therefore, it is not only the outcome of dominance contests that can affect metabolic traits relative to the rest of the population, but also the intensity of such contests with the behaviour of the opponent playing an important role in determining surplus AS available to an individual. Further, while dyadic contests offer a useful starting point for understanding links among metabolic traits, dominance and territoriality, interactions among conspecifics in nature may display differing social dynamics. In the wild, for example, networks of social interactions or dynamically shifting associations among competing neighbours may form complex social hierarchies as opposed to simple dominant/subordinate relationships (Stamps & Krishnan 2001; Sloman & Armstrong 2002). Additional work is therefore needed to examine the role of traits such as RMR and AS in more complex social environments with potential implications for selection on specific traits.

DO INDIVIDUALS RECOGNISE AND RESPOND TO PREVIOUS OPPONENTS?

Fish exhibited a stronger metabolic response when exposed to a prior competitor as compared to a stranger, but displayed similar levels of activity and aggression during exposures, regardless of the degree of competitor familiarity. This suggests that the increase in metabolic rate elicited upon exposure to the previous competitor involves an autonomic stress response (Wendelaar Bonga 1997; Sloman *et al.* 2000). This stress response could be in preparation for an agonistic encounter, and the especially pronounced response among dominants could represent a metabolic cost associated with hierarchy maintenance. It is unclear why this response was not elicited upon exposure to a stranger. A possible explanation is that familiar individuals have known 'motivations' (e.g. to claim disputed territory), have knowledge of the territory value, and are aware of the owner's state of vigilance and ability to defend the territory. These factors could make familiars a more apparent threat and therefore an aggressive encounter more likely (Müller & Manser 2007; Schradin, Schneider & Lindholm 2010). The motivations of a stranger are uncertain, and so an immediate stress response in preparation for engagement is less likely to occur. It is also possible that the response to each category of conspecific may change with an increased level of familiarity beyond the 1 h period of exposure used in the current study. Additionally, the change in context between trials (i.e. movement from the arena to adjacent chambers) may have altered the response to familiar versus unfamiliar competitors. Nevertheless, it is clear that individuals showed the greatest metabolic response to their prior competitor.

The observations that: (i) fish showed a greater metabolic response when exposed to a familiar competitor; and (ii) familiarity did not affect the amount of displayed aggression, both oppose our prediction that individuals would display less aggression towards a familiar competitor. In several territorial species, it has been observed that animals display less aggression to neighbours (Ydenberg, Giraldeau & Falls 1988). Exceptions have been documented, however, where individuals direct more aggression towards neighbours, as compared to strangers (Temeles 1994; Müller & Manser 2007; Schradin, Schneider & Lindholm 2010). For settlement-stage damselfishes, access to the safest available habitat can decide whether or not an individual will survive the severe predation present in reef habitats. Thus, competition among individuals should be intense. In the current study, dominants in arena trials almost always continued some degree of aggression towards subordinates throughout the entire arena trial, suggesting they continue to be aggressive even against a submissive opponent.

For both dominants and subordinates, activity and aggression displayed within respirometers during exposure to conspecifics did not correlate with changes in metabolic rate. In a competitive interaction, the cost of activity may be obscured by the effects of stress on oxygen consumption. Still, in examining the maximal rates of oxygen uptake during the exposure to conspecifics within adjacent respirometers we can estimate the maximal cost of aggression in relation to AS. For example, during exposures to a previous competitor, the increase in metabolic rate resulted in a 14·96% decrease in available AS for dominants. Exposure to a previous competitor only resulted in a 4·49% decrease in AS for subordinates. However, this decrease was in addition to the 17·39% decrease in AS already experienced due to the increase in RMR observed following the arena dominance trials. Therefore, the total decrease in available AS for subordinates was 21·88%. While this represents a potentially important reduction in aerobic capacity available for other energetically demanding tasks, it also suggests that metabolic rate during aggressive interactions does not approach MMR, as estimated following forced exercise (Thorpe, Taylor & Huntingford 1995). These results should be interpreted with caution, however, as there are several important differences between the interactions of fish through the walls of adjacent respirometers and competitive interactions in the arena or in the wild. Interactions in the arena sometimes involved chases, which were not possible to perform in respirometers, and these behaviours may cause especially large increases in metabolic rate (Ros, Becker & Oliveira 2006; Briffa & Sneddon 2007; Seebacher, Ward & Wilson 2013). Interestingly, in *c.* 20% of trials, the subordinate individual became the most aggressive when re-paired with the same fish in adjacent respirometers. The fact that exposure to conspecifics within respirometers precludes physical contact between competitors is likely to affect the escalation of aggressive interactions from displays to attacks, thus allowing individuals that would otherwise become subordinate to possibly appear dominant. Lastly, while fish in adjacent respirometers displayed aggression towards each other, there was no coral refuge, which may have affected the outcome of interactions or the amount of aggression displayed.

CONCLUDING REMARKS

There are a number of complex links between metabolic traits and behaviours associated with dominance and intraspecific competition in juvenile damselfishes. An increased AS is advantageous for acquiring preferred territory, but at the same time, the intensity and outcome of the competitions can drive subsequent energy expenditure and available AS via the effects of social stress. A promising avenue for future research will be to examine how metabolic capacity of conspecifics is modulated during aggressive interactions, how this may disrupt performance hierarchies, and the importance of metabolic traits for selective processes. Also requiring further study is the effect of environmental conditions (e.g. habitat quality, temperature) on the importance of AS and metabolic rate in the context of intraspecific competition for territory (Killen *et al.* 2013).

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Data accessability

Data deposited in the Dryad repository: http://doi.org/10.5061/dryad.7gc05 (Killen *et al.* 2014).

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Supporting Information

Additional Supporting information may be found in the online version of this article:

Fig. S1. Mean oxygen uptake rates during measurements of precontest metabolic traits. Dark circles represent individuals that went on to be dominant in dyadic contests; open circles represent those that went on to be subordinate. The *x*-axis represents time since the cessation of exhaustive exercise. Maximal metabolic rate (MMR) at time zero was estimated as the y-intercept of using a three-parameter exponential function for each fish. Routine metabolic rate (RMR) for individuals was estimated from the mean of the final three points along the right-hand side of the graph, at times 110, 130 and 150 min. Aerobic scope for each individual was calculated as MMR-RMR.

Fig. S2. Relationship between the relative change in oxygen uptake (as a percentage of precontest RMR) of individual and their aggression relative to their competitor in the dyadic dominance contests. Individuals with a negative score received a greater amount of aggression than they expressed. Dark circles represent dominant individuals; open circles represent subordinate individuals. A linear mixed model with fish identity nested within pair reveals a significant effect of the relative difference in aggression on the change in oxygen uptake post-contest (see Results).

Video S1. Example of aggression displayed between two rival juvenile Ambon damselfish competing for a small piece of coral. This interaction was filmed from within the tank using an underwater camera and was not used to collect data for the current study.