Journal of FISH BIOLOGY

Journal of Fish Biology (2016)
doi:10.1111/jfb.12890, available online at wileyonlinelibrary.com

The influence of status and the social environment on energy stores in a social fish

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(Received 30 April 2015, Accepted 17 November 2015)

This study explores how muscle and liver energy stores are linked with social status and the social environment in *Neolamprologus pulcher*, a cooperatively breeding fish that lives in colonies comprised of up to 200 distinct social groups. Subordinate muscle energy stores were positively correlated with the number of neighbouring social groups in the colony, but this pattern was not observed in dominant *N. pulcher*. Furthermore, liver energy stores were smaller in dominants living at the edge of the colony compared with those living in the colony centre, with no differences among subordinates in liver energy stores. Subordinate *N. pulcher* may build up large energy stores in the muscles to fuel rapid growth after dispersal, which could occur more frequently in high-density environments. Dominant *N. pulcher* may use the more easily mobilized energy stores in the liver to fuel daily activities, which could be more energetically demanding on the edge of the colony as a result of the increased predation defence needed on the edge. Overall, this study demonstrates that both subordinate and dominant physiology in *N. pulcher* varies with characteristics of the social environment. Furthermore, dominant and subordinate energy storage strategies appear to differ due to status-dependent variation in daily activities and variation in the need to prepare for future reproductive or dispersal opportunities.

Key words: colony; cooperative breeding; dispersal; liver; muscle; *Neolamprologus pulcher*.

INTRODUCTION

Individuals often store energy during times of high food availability or low energetic demands and then later use these stores for energetically costly activities such as reproduction, growth and migration (Dawson & Grimm, 1980; Jørgensen *et al.*, 1997; Arrington *et al.*, 2006). While energy stores provide the resources necessary to carry

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out essential activities, unnecessarily large stores can reduce fitness by inhibiting mobility and predator avoidance (Witter *et al.*, 1994; Kullberg *et al.*, 2000; Almbro & Kullberg, 2008). Therefore, energy storage should depend on both current energetic demands and anticipated future energetic requirements. Active individuals often have smaller energy stores than individuals who are less active (Shine & Mason, 2005; Sopinka *et al.*, 2009). Furthermore, individuals with low current energetic demands, but who anticipate high energetic costs in the future (*e.g.* to support reproduction, dispersal or migration) should stockpile somatic energy stores (Doughty & Shine, 1998).

In group living species, dominance status often influences growth and energy stores (Abbott & Dill, 1989; Sloman *et al.*, 2000; Buchner *et al.*, 2004; Sopinka *et al.*, 2009). Subordinate individuals often grow more slowly than dominants, due to a variety of mechanisms including reduced food accessibility (Fausch, 1984; Sloman *et al.*, 2000) and increased physiological stress resulting from aggression by more dominant individuals (Gilmour *et al.*, 2005). Subordinates in several species with size-based dominance hierarchies have decreased somatic growth, which may reduce rank-related conflict with other individuals in their group [*Neolamprologus pulcher* (Trewavas & Poll 1952): Heg *et al.*, 2004; Hamilton *et al.*, 2005; Hamilton & Heg, 2008; *Amphiprion percula* (Lacépède 1802): Buston, 2003; *Amphiprion ocellaris* Cuvier 1830: Mitchell & Dill, 2005; *Paragobiodon xanthosoma* (Bleeker 1853): Wong *et al.*, 2007; *Centropyge bicolor* (Bloch 1787): Ang & Manica, 2010]. Subordinates may also suppress their reproduction to minimize reproductive conflict with dominant individuals (Bell *et al.*, 2014). If given the chance to ascend in dominance, these subordinates can grow rapidly (Heg *et al.*, 2004) and quickly increase their gonadal investment (Fitzpatrick *et al.*, 2006, 2008; Heg, 2008). Having a ready source of available energy for periods of intensive growth and gonad development is expected to be advantageous, as larger individuals are better able to defend a newly acquired territory or rank (Candolin & Voigt, 2001; Moore, 2009; Reddon *et al.*, 2011) and tend to have higher reproductive success (Olsson & Shine, 1996).

In addition to social rank within a group, the broader social environment should also influence energy storage. Stored energy is expected to be important in densely inhabited environments where individuals must frequently engage in energetically costly social interactions with individuals from neighbouring groups (Grantner & Taborsky, 1998; Taborsky & Grantner, 1998; Guderley & Couture, 2005; Castro *et al.*, 2006). For colonially breeding organisms, individuals on the edge of the colony may also deplete their energy stores more quickly than individuals in the centre of the colony, as they are likely to be more active against predators (Brown & Brown, 1987; Forster & Phillips, 2009) and receive less cooperative defence from neighbouring groups (Schädelin *et al.*, 2012; Jungwirth *et al.*, 2015).

In teleosts, muscles and the liver are important reservoirs for energy stores and fuel reproduction, growth and energetically costly activities (Chellappa *et al.*, 1989; Huntingford *et al.*, 2001). Because energetic stores in the liver are easily mobilized (Chellappa & Huntingford, 1989), liver stores may be more important in fuelling aggressive contests, defence and daily activities compared with muscle stores (Chellappa & Huntingford, 1989; Sopinka *et al.*, 2009). In contrast, energy stores in muscles and other somatic tissues are much larger than those in the liver (Dawson & Grimm, 1980; Jørgensen *et al.*, 1997; Huntingford *et al.*, 2001) and appear to be used in conjunction with liver stores to fuel costly but long-lasting endeavours such as reproduction and somatic growth (Jørgensen *et al.*, 1997; Huntingford *et al.*, 2001).

Because these two sources of energy may be used for different purposes, energetic stores in the liver and in the muscles may vary with respect to different individual or environmental characteristics.

Variation in the social environment has not only been linked to differences in individual behaviour (Kutsukake & Clutton-Brock, 2008; Hellmann & Hamilton, 2014; Hellmann *et al.*, 2015*a*) and reproductive patterns (Petrie & Kempenaers, 1998; Cohas *et al.*, 2006; Hellmann *et al.*, 2015*b*), but is also expected to induce physiological variation among individuals. This study evaluated how liver and muscle energy stores correlate with both individual characteristics (*i.e.* sex and status) and characteristics of the external social environment (*i.e.* spatial location on the edge *v.* centre of the colony, density of neighbouring groups and proximity of the closest neighbouring group) in wild groups of *N. pulcher*, a cooperatively breeding fish native to Lake Tanganyika, East Africa. *Neolamprologus pulcher* form colonies of two to 200 territorial groups, each with a dominant pair and one to 20 subordinate group members that form size-based dominance hierarchies (Wong & Balshine, 2011). Subordinate males can strategically restrain their growth when close in size (standard length, L_S) to other group members and increase in size quickly if they have an opportunity to ascend in the dominance hierarchy (Heg *et al.*, 2004). Both sexes show signs of subordinate reproductive suppression (Fitzpatrick *et al.*, 2006; Heg, 2008). A previous study in this species linked liver size to variation in daily activity levels (Sopinka *et al.*, 2009).

Liver energy stores are expected to reflect variation in daily activity. Specifically, subordinates were predicted to have relatively larger liver stores than dominants, as hepatic mass decreases with increasing activity in this species and subordinates tend to be less active than dominants (Sopinka *et al.*, 2009). Liver stores were also predicted to be smaller on the edge of the colony compared with the centre, potentially due to higher antipredator defence on the edge of the colony (Brown & Brown, 1987; Forster & Phillips, 2009), and smaller in areas with closer neighbouring groups, due to an increased number of social interactions with neighbouring groups (Bergmüller *et al.*, 2005). Muscle energy stores were predicted to vary more in response to differences in future reproductive and dispersal opportunities. Because subordinates require energy stores for future periods of rapid growth, subordinates were expected to have large muscle energy stores, particularly in dense social areas where opportunities for dispersal and dominance ascension in nearby social groups are likely to be high (Heg *et al.*, 2008). This effect should be particularly strong for males, who disperse more frequently in this species (Stiver *et al.*, 2007).

MATERIALS AND METHODS

FIELD COLLECTION

Between February and April 2013, 51 *N. pulcher* groups were sampled in Kasakalawe Bay, Lake Tanganyika, East Africa (8° 46′ S; 31° 46′ E) using scuba. Groups were located in seven different colonies or subpopulations ranging in depth between 11 and 13·5 m. Colonies consist of a clustering of distinct social groups each defending a rocky territory and are separated from each other by large areas of sand and rocky rubble that are uninhabited by *N. pulcher* (Wong & Balshine, 2011). Groups were identified as being on the edge of the colony if half or more of that group's territory bordered an unoccupied area with no other conspecific groups within 10 m on that side of the territory (Hellmann *et al.*, 2015*b*).

Using fence nets and hand-nets, all sexually mature dominant and subordinate individuals [mature gonads and close to 35 mm L_S (Taborsky, 1985)] were captured. *Neolamprologus pulcher* were identified as part of the focal group if they swam repeatedly under the territory rocks without eliciting aggression from other *N. pulcher* within the territory boundaries. Within each focal group, dominant and subordinate *N. pulcher* were differentiated based on size. Dominance is very strongly linked to body size in this species (Reddon *et al.*, 2011; Dey *et al.*, 2013). The largest male and female *N. pulcher* are almost always the dominant pair (Wong & Balshine, 2011). Parentage analysis on a sub-set of these groups confirmed that the dominant individuals were correctly identified and collected in conjunction with their home territory (Hellmann *et al.*, 2015*b*). After collection, the distance to all conspecific neighbours within a 3 m radius was measured and territory size, which was defined as the area of rocks defended by the dominant male and female, was recorded.

All collected *N. pulcher* were brought to the surface, where adult body mass (to the nearest 0·001 g) and L_S (to the nearest 0·01 mm) were measured. *Neolamprologus pulcher* were euthanized by immersion in a lethal concentration of benzocaine (ethyl p-aminobenzoate, 1·0 μg ml^{-1}), and the livers and gonads were removed from adults and weighed. A section of muscle spanning from the base of the dorsal fin to the base of the anal fin was removed, packed on ice, transferred to the Lake Tanganyika Research Unit in Mpulungu and stored between −20 and −80° C until they were later analysed for energetic density. In total, hepatic mass was measured in 152 individuals, including dominant males ($n = 41$), dominant females ($n = 37$), subordinate males ($n = 26$) and subordinate females ($n = 48$) across 51 groups, including both edge groups ($n = 17$) and centre groups ($n = 34$). Hepatic mass was used as a proxy for liver energy stores, as hepatic mass is tightly linked with liver energy stores and body condition (Hilton, 1982; Arndt, 2000; Chippari-Gomes *et al.*, 2005). It is possible that handling procedures, including the time between capture and anaesthetic, may have altered the measured physiological variables; however, all reported results are comparisons of relative stores between individuals who were subjected to the same handling procedures and there is no *a priori* reason to suspect that handling procedures would create biases between comparison groups.

CALORIMETER ANALYSIS FOR MUSCLE SAMPLES

Muscle samples were analysed for energetic content by measuring the number of calories dry g^{-1} of tissue (energetic density). All muscle samples were thawed, weighed and placed in a desiccating oven (60–70° C) for drying. Samples were dried for 24–72 h until the sample mass was within 2% of the previous day's mass. Samples were removed from the oven and immediately ground into a fine powder using a mortar and pestle. Because the samples were too small to run individually, samples were pooled using equal amounts of homogenized powder from each individual (Dubreuil & Petitgas, 2009). Individuals were pooled based on status, sex, spatial location (edge *v.* centre of colony) and number of neighbouring groups. Each pooled sample consisted of two to four individuals. When the number of neighbouring groups within 3 m differed for individuals within a pooled sample, values were averaged across all individuals in that sample.

Once pooled, ground muscle samples were mixed with benzoic acid [a standard of known energetic density: 26·436 kJ g^{-1} (6318·4 cal g^{-1})] until the total composite sample mass was >1 g. The mass of both muscle tissue and benzoic acid in each sample was recorded. Composite samples of muscle tissue and benzoic acid were compressed into a pellet and combusted using a Parr 6400 Automatic Isoperibol Calorimeter (Parr Instrument Company, 2010; www.parrinst.com) to determine energetic density (cal g^{-1} of dry mass converted into kJ g^{-1}). This technique, previously used for tissues of low energetic density (Doyle *et al.*, 2007), increased the total calories in each pooled sample above 20·92 kJ g^{-1} (5000 cal g^{-1}), which is required for the Parr 6400 Automatic Isoperibol Calorimeter to generate precise estimates of energetic density. Values of muscle tissue energetic density (cal g^{-1} of dry mass converted into kJ g^{-1}) include energy released from the combustion of proteins, carbohydrates and lipids. As lipids are the densest form of energy, however, values of total energetic density are highly sensitive to variation in lipid stores (Anthony *et al.*, 2000). In total, 57 pooled muscle samples were processed, including pooled samples for dominant males ($n = 17$), dominant females ($n = 16$), subordinate males ($n = 10$) and subordinate females ($n = 14$). Offering evidence that muscle energetic densities from pooled samples were equivalent to those from non-pooled samples, the subordinate energetic density of muscle tissue in pooled samples that were frozen after collection was statistically equivalent to non-pooled samples of 17 *N. pulcher* subordinates collected from the same field site and then sun-dried after collection (Mann–Whitney U-test: $U = 187$, $P > 0{\cdot}05$). This suggests that pooling samples and freezing samples does not strongly alter sample values compared with non-pooled, sun-dried samples.

STATISTICAL ANALYSIS

General linear models (GLMs) were used to test predictors of muscle energy stores (cal g^{-1} of dry mass converted into kJ g^{-1}). Spatial location within the colony (centre *v.* edge), the density of neighbouring groups (number of conspecific groups within 3 m) and sex were tested as fixed effects in the model. To account for any potential differences in muscle energetic density due to pooling, the number of individuals pooled per sample was included in the model. Mean L_S of the pooled individuals was also included in the model to account for the variation in energetic density due to differences in size. To compare hepatic and gonadal mass (individual samples) with muscle energetic density (pooled samples), hepatic mass and gonadal mass were averaged for each individual in the pooled muscle samples.

General linear mixed models (GLMMs) were also used to test the influence of spatial location, sex and distance to the closest neighbour on hepatic mass. The density of neighbouring groups was not used in this analysis because it was highly correlated with the distance to the closest neighbour, and evaluation of model fit using AIC values demonstrated that model fit was improved by including distance to the closest neighbour over density. The non-hepatic mass of the individual (total mass − liver mass) was included in the liver model as an additional fixed effect to standardize for variation in individual size. Non-hepatic mass was used because it is independent of hepatic mass. Total mass is correlated with hepatic mass and so the use of total mass can generate the appearance of a positive relationship between body size and liver size when one does not exist (Christians, 1999; Tomkins & Simmons, 2002). Finally, the focal group of each individual was included as a random effect. For both liver and muscle energy stores, models for dominants and subordinates were run separately, as there were significant differences in both muscle and liver stores between dominants and subordinates. For both models, interactions were tested and non-significant interactions were removed. Analyses were performed in R 3.0.3 with the lme4 package (Bates *et al.*, 2013; R Core Team; www.r-project-org).

ETHICAL NOTE

Neolamprologus pulcher is neither endangered nor threatened. The physical territories were minimally disturbed during collection and new social groups occupied the collected groups' territories within 1–2 days post-collection. All methods, including euthanasia techniques, were approved by the Zambian Department of Fisheries, The Ohio State University IACUC (protocol ID 2008A0095) and the Animal Research Ethics Board of McMaster University (Animal Utilization Protocol Number 10-11-71). These procedures adhered to the guidelines of the Canadian Council for Animal Care and the Animal Behaviour Society.

RESULTS

MUSCLE ENERGETIC DENSITY

Muscle energy density (dry mass) was significantly lower in dominants compared with subordinate individuals [dominants: mean ± s.e. $= 13{\cdot}154 \pm 0{\cdot}301$ kJ g^{-1}; subordinates: mean ± s.e. $= 14{\cdot}698 \pm 0{\cdot}280$ kJ g^{-1}; GLM: $t_{52} = 3{\cdot}73$, $P < 0{\cdot}001$; Fig. 1(a)]. Among dominants, energetic density in muscle tissue did not vary between males and females, with the density of neighbouring groups or with the relative location of the group within the colony (centre *v.* edge; Table I). For subordinates, muscle energetic

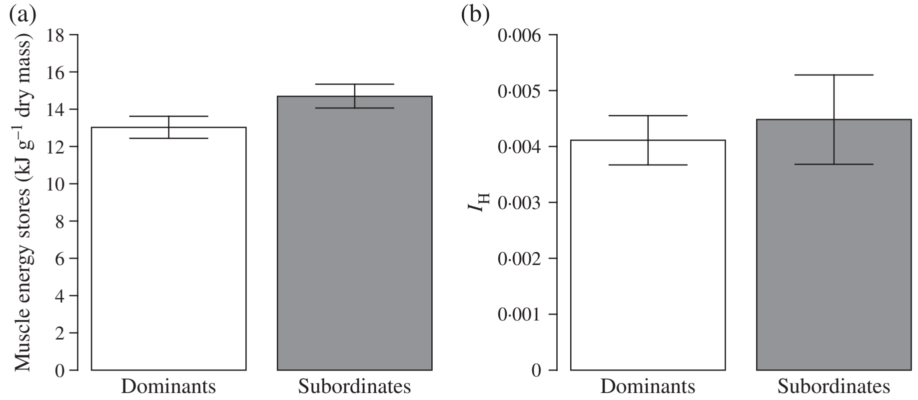

FIG. 1. (a) Muscle energy stores and (b) hepato-somatic indices (I_H) in dominant and subordinate *Neolamprologus pulcher*. Values are means with 95% C.I. In both cases, values were significantly higher in subordinates compared with dominants ($P<0{\cdot}05$).

density significantly increased as the density of neighbouring groups increased (Fig. 2), but did not vary between individuals living on the edge *v.* the centre of the colony (Table I). Subordinate males tended to have higher muscle energetic density than subordinate females, although this pattern did not reach significance (Table I).

There was no correlation between muscle energetic density and absolute or relative liver size of the individuals (GLM; absolute: $t_{43} = -0{\cdot}88$, $P > 0{\cdot}05$; relative: $t_{46} = 1{\cdot}37$, $P > 0{\cdot}05$). Among males, muscle energetic density significantly increased as absolute gonadal mass decreased (GLM: $t_{18} = -2{\cdot}62$, $P < 0{\cdot}05$) and tended to increase as relative gonadal mass decreased (GLM: $t_{18} = -1{\cdot}78$, $P > 0{\cdot}05$). For females, there was no significant correlation between muscle energetic density and absolute or relative gonadal mass (absolute: GLM: $t_{18} = -0{\cdot}78$, $P > 0{\cdot}05$; relative: GLM: $t_{18} = -0{\cdot}82$, $P > 0{\cdot}05$).

HEPATIC MASS

Hepatic mass (after controlling for non-hepatic mass) was smaller in dominants compared with subordinates [dominants: mean ± S.E. = 0·41 ± 0·02%; subordinates:

TABLE I. Results of full models (general linear model, GLM) testing total energetic density (kJ g^{-1} dry mass) in muscle tissue, controlling for variation in the number of individuals pooled per sample and for variation in standard length of the pooled individuals. Dependent variables tested include spatial location in the colony (centre *v.* edge territory), density of neighbouring groups within 3 m and sex. Models were run separately for dominant and subordinate individuals. Interactions between dependent variables were tested and all non-significant interactions were removed from the model.

	Dominant energetic density		Subordinate energetic density	
Predictors	t_{25}	P	t_{17}	P
Spatial location	0·96	>0·05	−0·05	>0·05
Density	−0·81	>0·05	2·57	<0·05
Sex	1·34	>0·05	−1·83	>0·05

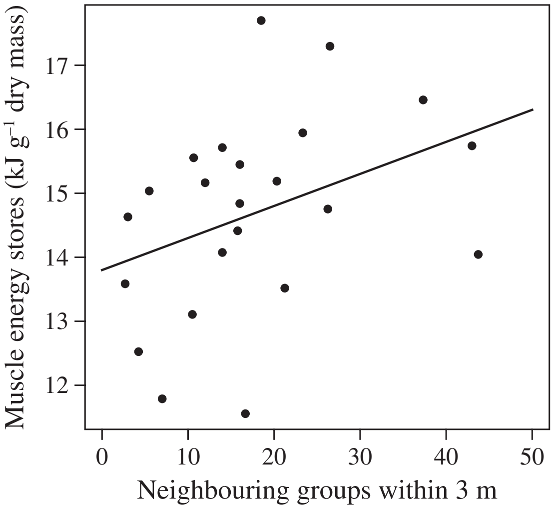

FIG. 2. Muscle energy stores of subordinates in relation to the density of neighbouring groups within 3 m. The curve was fitted by: $y = 0.05x + 13.8$.

mean ± S.E. = 0·45 ± 0·04%; GLMM: $t_{100} = 2.03$, $P < 0.05$; Fig. 1(b)]. Among dominant individuals, there was a significant interaction between spatial location (centre *v*. edge) and distance to the nearest neighbour, whereby hepatic mass significantly increased as the distance to the nearest neighbour increased, but this effect was only apparent for individuals living on the edge of the colony [Table II and Fig. 3(a)]. There was no significant relationship between hepatic mass and distance to the nearest neighbour for dominants in the centre of the colony [Table II and Fig. 3(b)]. Dominant hepatic mass did not vary between sexes. For subordinate individuals, there were no differences in hepatic mass due to location on the edge *v.* centre of the colony, the distance to the nearest neighbour or sex (Table II).

There were no significant relationships between relative liver size (hepatic mass:non-hepatic mass) and gonad size (gonad mass:non-gonadal mass) for dominant males (GLMM: $t_{37} = 0.37$, $P > 0.05$) dominant females ($t_{33} = 0.96$, $P > 0.05$) or subordinate

TABLE II. Results of full model (general linear mixed model, GLMM) testing hepatic mass, controlling for non-hepatic mass. Dependent variables tested include spatial location in the colony (centre *v.* edge territory), distance to closest neighbour and sex. Models were run separately for dominant and subordinate individuals. Interactions between dependent variables were tested and all non-significant interactions were removed from the model

	Dominant hepatic mass		Subordinate hepatic mass	
Predictors	t_{43}	P	t_{36}	P
Spatial location	−2·70	<0·01	−0·69	>0·05
Closest neighbour	−1·47	>0·05	−0·41	>0·05
Sex	−0·75	>0·05	0·81	>0·05
Location × closest neighbour	3·21	<0·01	–	–

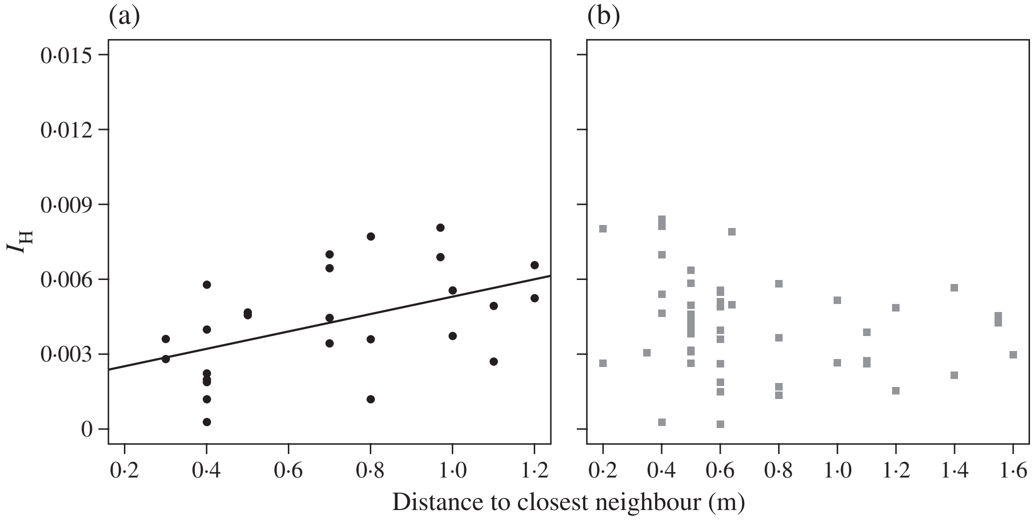

FIG. 3. Dominant fish hepato-somatic indices (I_H) (a) were positively correlated with distance to the nearest neighbour on the edge of the colony ($y = 0{\cdot}0031x + 0{\cdot}00224$) but (b) did not vary with distance to the nearest neighbour in the centre of the colony.

males ($t_{72} = -1{\cdot}06$, $P > 0{\cdot}05$). For subordinate females, however, relative liver size significantly decreased as relative gonad size increased ($t_{14} = -2{\cdot}19$, $P < 0{\cdot}05$).

DISCUSSION

This study explored variation in muscle and liver energy stores relative to individual status and sex, as well as characteristics of the social landscape, in the social cichlid *Neolamprologus pulcher*. Subordinates had higher energy stores in both the liver and the muscle tissues compared with dominant individuals, even after controlling for differences in body size. Furthermore, subordinate muscle stores increased as the density of neighbouring groups increased, while dominant muscle stores showed no relationship with the density of neighbouring groups. Instead, liver size in dominant individuals was influenced by the distance to the nearest neighbour and the spatial location of their territory. On the edge of the colony, liver size among dominants increased as distance to the nearest neighbour increased, although this trend was not evident for dominants in the centre of the colony. Collectively, these results suggest that energy storage varies with the social environment and that this variation depends upon the social status of the individual.

In this study, hepatic mass varied with the social environment in dominants, whereas muscle energetic stores varied in response to the social environment in subordinates. Liver glycogen and lipid levels (and therefore, hepatic mass; Hilton, 1982; Arndt, 2000; Chippari-Gomes *et al.*, 2005) are often smaller than energy stores found in the muscles, but vary dynamically with daily activity (Chellappa *et al.*, 1989; Arndt, 2000; Arrington *et al.*, 2006; Sopinka *et al.*, 2009) and tend to be smaller in more active individuals in this species (Sopinka *et al.*, 2009). Muscle tissues represent one of the largest stores of energy in the body and fuel daily activities and maintenance as well as long-term priorities such as dispersal and maturation (Dawson & Grimm, 1980; Chellappa *et al.*, 1989; Arrington *et al.*, 2006). Therefore, these results suggest that smaller energy stores in the liver may vary in response to variation in daily activities in dominants, whereas larger energy stores in the muscles may vary in response to opportunities for life stage changes, such as dispersal and dominance ascension, for subordinates.

In this study, dominant individuals had relatively smaller livers than subordinates; this relationship was weakly significant, but is consistent with results of a prior study on liver size in this species (Sopinka *et al.*, 2009). It is also consistent with previous studies demonstrating that dominants are generally more active than subordinates in this species (Sopinka *et al.*, 2009), assuming prominent roles in territory defence (Desjardins *et al.*, 2008), within-group policing (Dey *et al.*, 2013) and reproduction (Hellmann *et al.*, 2015*b*). Dominant liver size was smaller on the edge of the colony relative to the centre, suggesting that dominants are more active on the edge of the colony compared with the centre (Sopinka *et al.*, 2009). This may be a result of an increase in predation and defence effort by dominants on the edge of the colony. Colonial breeding is frequent in many fish species and appears to have evolved to provide antipredator benefits [*Lepomis macrochirus* Rafinesque 1819: Dominey, 1981; *Malacanthus plumieri* (Bloch 1786): Baird & Baird, 1992; *Abudefduf abdominalis* (Quoy & Gaimard 1825): Tyler, 1995]. These antipredator benefits are often due to increased overlap in defended areas (Dominey, 1981), allowing individuals to expend less energy on antipredator behaviour. In many colonial species, however, individuals living on the edge of the colony are vulnerable to predators approaching from the outside of the colony (Brown & Brown, 1987; Forster & Phillips, 2009), particularly because neighbours on the inside of the colony are unlikely to aid edge groups in defending against predators coming from the outside of the colony (Schädelin *et al.*, 2012; Jungwirth *et al.*, 2015). Because dominants on the edge of the colony may have a large area to defend without help from neighbours, they may expend more energy engaging in costly defensive behaviours than dominants in the centre.

Among dominants living on the edge of the colony, liver size was smaller when conspecific neighbours were closer. Dominants with close neighbours probably expend more energy interacting with individuals in neighbouring groups compared with dominants that have more distant neighbours (Bergmüller *et al.*, 2005). Clusters of groups on the edge of the colony may also attract more predators than isolated groups on the edge of the colony, thereby increasing the amount of defence performed by the dominants (Heg *et al.*, 2008). Interactions with both conspecifics and with predators are probably energetically costly, and individuals who frequently interact with both are expected to expend high levels of energy.

While subordinate liver or muscle energy stores did not vary between the edge and the centre of the colony, subordinates did have higher muscle energetic stores in denser areas. A high density of neighbouring individuals or groups has been linked to lower food availability (Desy & Batzli, 1989) or increased opportunities for reproductive activities (Petrie & Kempenaers, 1998; Griffith *et al.*, 2002; Hellmann *et al.*, 2015*b*), both of which would probably be associated with reduced energetic stores. Instead, variation in muscle energy stores in subordinates may be due to differences in dispersal opportunities between high-density and low-density areas. Across taxa, individuals will often disperse to the closest neighbouring groups (Russell & Rowley, 1993; Doolan & MacDonald, 1996; Heg *et al.*, 2008; Drewe *et al.*, 2009) and the number of dispersal opportunities tends to increase as the density of neighbouring groups increases (Heg *et al.*, 2008). In situations in which dispersal is likely, subordinates would benefit from having large energy stores to allow for rapid periods of growth and gonadal development (Fitzpatrick *et al.*, 2006), which would increase success when fighting conspecific competitors and courting mates (Candolin & Voigt, 2001; Moore, 2009; Reddon *et al.*, 2011). As unnecessarily high energy stores can reduce survival rate by reducing the ability to escape predators (Kullberg *et al.*, 2000; Almbro & Kullberg, 2008), however, it may not be advantageous for subordinates with a low likelihood of dispersing to retain these energy stores. Because males disperse more often in this species (Stiver *et al.*, 2007), male subordinates were expected to have higher energy stores compared with female subordinates, which is consistent with the results of this study.

This study is novel in its demonstration that both dominant and subordinate energy allocation strategies vary in response to the social landscape. The results of this study are consistent with the hypothesis that subordinates build large amounts of muscle energy stores in high-density environments to accommodate increased dispersal opportunities and that dominants use liver energy stores, particularly at the edge of the colony, to fuel energetically costly daily activities. Furthermore, these results suggest that dominants vary energy stores in accordance with current demands, whereas subordinates adjust their energy stores to plan for potential future energetic needs. Collectively, this study demonstrates that energy stores in teleosts are not independent of the social context and may be integral to success within both the physical and social landscape.

The authors would like to thank C. Katongo (University of Zambia, the Mpulungu Department of Fisheries) and the staff of the Tanganyika Science Lodge for their logistical support of the field research. This research was supported by NSERC Discovery Grant, an Ontario Innovation Trust and a Canadian Foundation for Innovation grants to S.B., a Journal of Experimental Biology Travelling Fellowship to C.M.O. and McMaster School of Graduate Studies and Canadian Society of Zoologists research grants to A.R.R. C.M.O. was supported by an E. B. Eastburn Postdoctoral Fellowship. J.K.H. and I.Y.L. were supported by The Ohio State University Fish Systematics Endowment and the SciFund Challenge. J.K.H. was supported by American Academy of Underwater Sciences and Animal Behaviour Society. A.R.R. was supported by a Margo Wilson and Martin Daly Ontario Graduate Scholarship. S.B. is supported by the Canada Research Chairs Programme. Thanks are also extended to the Hamilton laboratory and two anonymous referees for comments on earlier drafts of this manuscript.

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