

Article

The benefits of being dominant: health correlates of male social rank and age in a marmot

Kenta UCHIDA^a, Rachel NG^a, Samuel A. VYDRO^a, Jennifer E. SMITH^{a,b}, and Daniel T. BLUMSTEIN ^{a,c,*}

^aDepartment of Ecology & Evolutionary Biology, University of California, Los Angeles, CA 90095-1606, USA,

^bDepartment of Biology, Mills College, Oakland, CA 94613, USA and ^cThe Rocky Mountain Biological Laboratory, Crested Butte, CO 81224, USA

*Address correspondence to D.T. Blumstein. E-mail: marmots@ucla.edu

Handling editor: Zhi-Yun JIA

Received on 19 February 2021; accepted on 22 April 2021

Abstract

The benefits of dominance may not come without costs, particularly for males. For example, the “immunocompetence handicap hypothesis” states that males with enhanced mating success allocate resources to enhance reproductive output at a cost to their current health, whereas the “resource quality hypothesis” predicts that high-ranking males may benefit from increased reproduction and good health. Whereas the predictions from each have been well tested in captive animals and in a variety of highly social primates, fewer studies have been carried out in free-living, facultatively social animals. Using adult male yellow-bellied marmots (*Marmota flaviventer*), we evaluated predictions of these hypotheses by examining the relationship between social rank and 2 health indicators—fecal glucocorticoid metabolite (FCM) levels, and neutrophil/lymphocyte (N/L) ratios—after accounting for variation explained by age, body mass, and seasonality. We found that higher-ranking males tended to have a lower N/L ratio (reflecting good health) than lower-ranking individuals, whereas FCM levels were not significantly related to rank. In addition, heavier male marmots had lower N/L ratios, whereas body mass was not associated with FCM levels. We also found that older adult males had lower FCM levels (reflecting less physiological stress) but higher N/L ratios than younger adults. Finally, we found that FCM levels decreased as the active season progressed and FCM levels were associated with the time of the day. Overall, our results suggest that socially-dominant male marmots enjoyed better, not worse health in terms of lower N/L ratios.

Key words: immunocompetence handicap hypothesis, life history trade-offs, N/L ratio, physiological stress, resource quality hypothesis

Animals face fundamental trade-offs between reproduction and survival. Life history theory predicts that because females are the limiting factor of parental investment (Trivers 1972), over which males will compete for reproductive opportunities. Such intra-sexual competition over access to limited females may be costly in terms of time and energy, generating trade-offs between male reproductive success and survival. This trade-off can be

explained by complex relationships that exist among behavioral traits and physiology (i.e., glucocorticoids [GCs] and overall health) in animals (Sapolsky et al. 2000; Réale et al. 2010). These relationships and their underlying mechanisms likely play a crucial ecological role, yet we still lack a fundamental understanding of how they trigger trade-offs in the decisions that males make in natural environments (Archie et al. 2012).

One hypothesis to explain these relationships is the “immunocompetence handicap hypothesis” (Folstad and Karter 1992) which states that when testosterone modulates sexual characteristics and behavioral traits that enhance male reproductive success (Folstad and Karter 1992), males reduce their resource allocation to overall health and thus have a suppressed immune system (Roberts et al. 2004). Such immunosuppression increases an individual’s vulnerability to pathogens and parasites. This hypothesis predicts that males with higher quality genes will have high testosterone but poor health because these individuals are allocating their resources more toward mating success rather than to current maintenance of their health.

Support for the immunocompetence handicap hypothesis is consistent with the hypothesis that chronic stressors can induce a rise in GC levels and this hormonal response compromises vertebrate immune systems (Davis et al. 2008). The elevated GC levels due to environmental stresses are also known to suppress the immune function of individuals by changing the leukocyte component of many vertebrates such as increasing the ratio of heterophils or neutrophils to lymphocytes (Davis et al. 2008), which increase the pathogen and parasite burden or reduce resistance to toxins (Holding et al. 2020). For example, an adverse effect of reduced health is also associated with higher parasite burden as well as more prominent secondary sexual characteristics in the lacertid lizard (*Psammotromus algirus*; Salvador et al. 1996) and red grouse (*Trichostonglyx lenuis*; Mougeot et al. 2006), respectively. In the case of group-living animals, male social rank is associated with health conditions such as GC levels (Muller and Wrangham 2004; Levy et al. 2020) and individual immune status (Archie et al. 2012). Although being dominant enables male individuals to enhance their reproductive success (Hoogland and Foltz 1982; Fabiani et al. 2004), high-ranking individuals may need to allocate more energy to maintaining dominance compared with low-ranking conspecifics, and this may result in immunosuppression (Van Lieshout et al. 2020).

Despite the logic of the immunocompetence handicap hypothesis, not all empirical studies have supported it (Goymann et al. 2004; Roberts et al. 2004; Osomo et al. 2010). For example, high-ranking individuals have lower stress levels and higher immune status than low-ranking conspecifics in a variety of mammals and birds (Lindström 2004; Gesquiere et al. 2011; Archie et al. 2012; Flies et al. 2016). If higher-ranking individuals are in the best body condition due to better access to resources (von Holst et al. 1999), the high social status might buffer the costs of competition such that dominant individuals are less physiologically stressed and have strong immunity compared with subordinates. This evidence of good health in high-ranking animals might be in part because their priority of access to resources compensates for exposure to stressors that might otherwise compromise the immune system (Sapolsky 2005; Diamond and Kingsolver 2011; Snyder-Mackler et al. 2020) which is essentially a “resource quality hypothesis.” Yet, there are relatively few studies that have examined the relationships among social status, stress hormones, and immunological status of individuals within and among years after considering body condition in facultatively group-living animals.

Measuring the overall health of free-ranging animals can be challenging, yet there are a number of minimally invasive measures available to gain insights into how animals cope with physiological responses to stressors (Smith et al. 2012; Hadinger et al. 2015; Gormally and Romero 2020). The perception of a stressful situation activates the sympathetic–adrenomedullary system and the hypothalamic–pituitary–adrenocortical (HPA) axis (Johnstone et al. 2012). Activation of the HPA axis stimulates the release of GCs (Johnstone et al. 2012), and their metabolites can be measured in

non-invasively collected feces (Hadinger et al. 2015). Fecal glucocorticoid metabolites (FCMs) are a particularly useful marker to measure GCs because feces are easy to obtain and represent an accumulated measure (e.g., over the course of about a day—see Smith et al. 2012) of an individual’s physiological stress state.

A more specific measure of immunocompetence is reflected by the ratio of neutrophils to lymphocytes (hereafter N/L ratio) because exposure to chronic stressors negatively impacts an individual’s immune status through the elevation of GCs (Pride 2005; Davis et al. 2008). Importantly, measures of white blood cell counts are associated with fitness consequences in free-living birds (Kilgas et al. 2006). In mammals, white blood cells accumulate over a much longer time period than those reflected by plasma GCs (Davis et al. 2008) and, thus, high N/L ratios reflect an immunological response to longer-term chronic stressors (Martin 2009).

Here, we examined the relationship between dominance rank and physiological conditions by studying FCM levels and N/L ratios to understand the underlying proximate mechanisms of trade-offs in an obligate hibernator, the yellow-bellied marmot *Marmota flaviventer*. Adult male marmots are particularly well-suited to assess the relationship between dominance rank and physiological conditions because they vary in their mating system from monogamous to polygynous (Armitage 2014) and live in various sized groups. We know that marmots become more socially selective as they age (Wey and Blumstein 2010; Smith et al. 2013) and these early behavioral patterns (e.g., play bouts) likely predict later dominance status (Blumstein et al. 2013). However, whereas we have known that high-ranking adult female marmots are more stressed and have larger litter sizes than low-ranking ones (Blumstein et al. 2016), the physiological correlates of dominance rank at adulthood is poorly understood for male marmots.

The immunocompetence handicap hypothesis assumes that maintaining dominance has health costs. If this could be used to explain marmot behavior, we expected that the highest-ranking males who enjoy the highest annual reproductive success (Huang et al. 2011) would suffer from increased FCM levels and N/L ratios. Because older marmots are typically socially dominant to younger males (Huang et al. 2011), we specifically investigated the relationships between our measures of health (FCM levels, N/L ratios) and the age of adult male marmots, predicting that older males would have higher N/L ratios and FCM levels than younger males.

An alternative hypothesis, which we refer to as the “resource quality hypothesis” (Diamond and Kingsolver 2011), predicts that the highest-ranking males should be in the best health condition and should have the lowest FCM levels and N/L values. There is also evidence for this hypothesis in obligately social mammals, particularly in species of primates and cooperatively breeding carnivores (Archie et al. 2012; Montgomery et al. 2018). In this case, body condition which is associated with social dominance is also expected to predict individual health. Thus, under this hypothesis, we expected that heavier males would have lower FCM levels and N/L ratios. We also predicted that both measures of health would decrease as the active season progressed and resource quality (e.g., food) increased because a previous study showed that, in a hibernating mammal, GCs were highest at the end of the active season (Reeder et al. 2004).

Materials and Methods

From 2002 to 2018, we collected physiological and behavioral data on wild marmots in and around the Rocky Mountain Biological Laboratory (RMBL), located in the Upper East River Valley, in

Gunnison County, Colorado, USA. Marmots have been studied at this location since 1962 (Blumstein 2013; Armitage 2014).

Physiological data

Physiological data were collected by live-trapping marmots in Tomahawk traps set at burrow entrances approximately every other week during the active season (May to August). Upon capture, we transferred each marmot into a canvas handling bag to be weighed, sexed, and, if necessary, marked with new ear tags and fur dye; the handling of each individual takes ~5–10 min. Ages of adult males were known for animals first trapped as pups and estimated for immigrant males who were initially recorded as 2 years old.

We collected fecal samples, when available, from the traps and immediately placed feces in Ziploc™ bags on ice after our arrival at each trap (≤ 2 h after defecation). Samples were frozen at -20°C within 2 h of collection and shipped on dry ice to the University of California Los Angeles (UCLA) for extraction. We used a validated (Smith et al. 2012) assay of FCMs where we first extracted GCs with an ethanol extraction (details in Blumstein et al. 2006), and then used a double-antibody ^{125}I radioimmunoassay kit (Wasser et al. 2000) to estimate FCMs in nanogram/gram.

Additionally, every 2 weeks, we aimed to collect up to 2.0 mL of blood per subject into heparin-coated tubes. Tubes were immediately placed on ice. Within 2 h of collection, blood smears were made from whole blood and stained with a Hema 3 Stat Pack (Thermo Fisher Scientific, Inc., Waltham, MA, USA). Neutrophils and lymphocytes were counted on blood smears using a $400\times$ compound microscope. The N/L ratio for each sample was determined by counting white blood cells until a total of 100 white blood cells were counted or until 30 min had passed, whichever occurred first.

Behavioral data

We used spotting scopes and binoculars to intensively observe marmots at 11 colony sites. We did this on most days during the times of peak activity (07:00–11:00; 16:00–19:30) from mid-April to mid-September. Observers recorded all occurrences of agonistic interactions (Martin and Bateson 1993). Agonistic interactions involved obvious aggression (biting, chasing, and fighting) and more subtle displacements of other individuals (full ethogram in Blumstein et al. 2009).

Following Huang et al. (2011), we calculated dominance hierarchies for members belonging to each social group based on the outcomes of agonistic interactions for which there was a clear winner and loser. We focused on the agonistic interactions among yearlings and adults. We used the Clutton-Brock Index (Clutton-Brock et al. 1972) to assign ranks based on each individual's relative number of wins and losses within its overall social group (mean social group size was 10.9). For these analyses, we defined the social group as including all members of the colony site in a given year because males defended 1 or more matriline within a colony site. We then normalized ranks to adjust for variation in social group size whereby the highest-ranking individual was given rank 1, whereas the lowest ranking individual was rank 0.

Statistical analysis

We fitted a series of linear mixed-effects models to examine the relationship between relative social rank and adult male marmots' FCM levels and N/L ratios. In all of our models, we included marmot identity, colony ID, and year as random effects to account for repeated measures on the same individuals and to account for the

possible effects of annual variation and social group size on these measures. For the FCM model, in addition to relative social rank, we also included sampling collection hour of the day, day of the year (Julian date), body mass, adult male age, and an interaction between relative rank and age as fixed effects in our model because previous research indicated that such factors explained some variation in marmot FCM levels (Smith et al. 2012). In the N/L ratio model, we included FCM levels as a fixed effect to assess the relationship between physiological stress level and N/L ratio, in addition to relative social rank, day of the year, body mass, age of adult males, and interaction between relative rank and age as fixed effects. The FCM levels, N/L ratio, and body mass data were log-transformed to normalize them for fitting the models. All continuous variables were standardized by zero-centering them. We verified that there was no multicollinearity by checking the variance inflation factors were < 3 with package “car” (Fox and Weisberg 2018). We visually confirmed that, after log transformation, the residuals of each model were relatively normal, q–q plots were relatively straight. We calculated marginal and conditional R^2 values using “MuMIn” (Barto 2020), to compare the goodness of fit of the model without and with random effects (Nakagawa and Schielzeth 2013). We used R software for all of our statistical analyses (R version 4.0.1; R Development Core Team 2020). The package “lme4” (Bates et al. 2015) was used to fit the mixed-effect models, and significance was calculated with “lmerTest” (Kuznetsova et al. 2017).

Results

Our data set to study variation in FCM levels included 213 complete records from 66 adult male marmots collected over 17 years. The interaction between social rank and age was not statistically significant and the conditional R^2 values were lower than the model without interaction term (Supplementary Table S1). Therefore, we refitted the model without this interaction and interpreted that model. Fixed effects explained some variation in FCM levels, but the conditional R^2 value (0.575), was substantially higher than the marginal R^2 value (0.094). After controlling for significant variation explained by the day of the year (Estimate = -0.072 , standard error (SE) = 0.022, $P < 0.001$; Table 1 and Figure 1D) and the time of the day (Estimate = 0.048, SE = 0.013, $P < 0.001$; Table 1 and Figure 1E), variation in FCM levels was not significantly explained by social rank (Estimate = -0.015 , SE = 0.015, $P = 0.326$; Table 1). Therefore, higher-ranking male marmots did not seem to have elevated fecal GC levels compared with lower-ranking males (Figure

Table 1. Independent variables explaining variation in FCMs levels of adult male yellow-bellied marmots

Fixed effects:	Estimate	SE	df	t value	P-value
(Intercept)	1.134	0.052	19.671	21.660	<0.001
Social rank	-0.015	0.015	149.954	-0.985	0.326
Age	-0.071	0.022	187.251	-3.266	0.001
Body mass	0.026	0.023	145.578	1.131	0.260
Day of year	0.048	0.013	193.723	3.695	<0.001
Time of day	-0.038	0.019	43.908	-2.042	0.047
	Conditional R^2		Marginal R^2		
	0.575		0.094		
Random effects:	Variance		SD	—	—
Individual ID	(Intercept)	0.003	0.052	—	—
Year	(Intercept)	0.029	0.170	—	—

Conditional and marginal R^2 are shown. Significant values in bold.

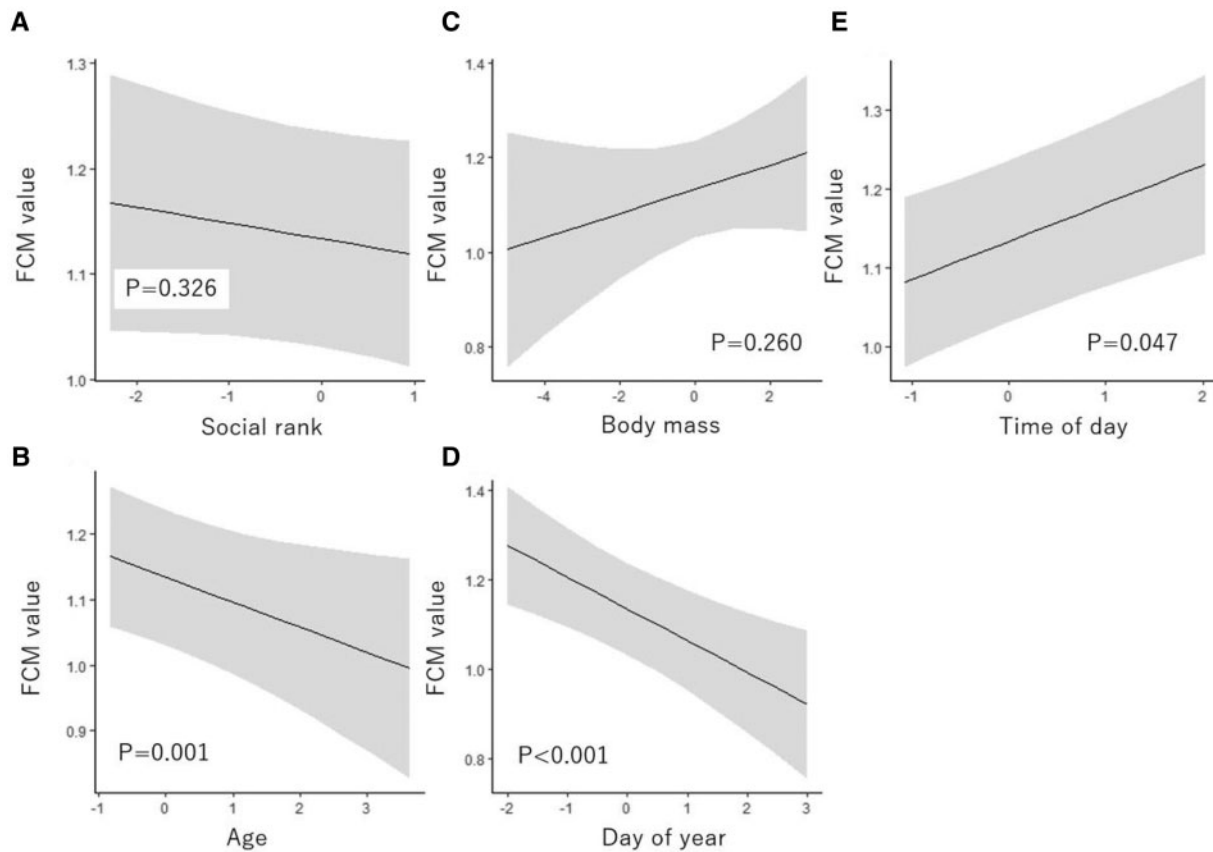


Figure 1. The relationships between standardized fixed effects [(A) Social rank, (B) age, (C) body mass, (D) day of year, and (E) time of day.] and log-transformed FCM levels. Each line was calculated using the predicted probabilities from the linear mixed-effects model (LMM) (see text for details). Buffers represent the 95% confidence interval. *P*-values are reported from the LMM.

1A). Additionally, FCM levels were not correlated with body mass (Estimate = 0.026, *SE* = 0.023, *P* = 0.260; Table 1 and Figure 1C). On the other hand, age was negatively associated with FCM levels (Estimate = -0.038, *SE* = 0.019, *P* = 0.047; Table 1 and Figure 1B); as males aged, their FCM levels declined.

Our data set to study variation in N/L ratios included 125 complete records from 54 adult male marmots collected 15 years. As with the FCM model, the interaction between social rank and age was not statistically significant and the conditional R^2 values were lower than the model without interaction term (Supplementary Table S2). Again, we refitted the model without the interaction term and interpreted the results of this simplified model. Fixed effects explained some variation in N/L ratios, but the conditional R^2 value (0.466) was substantially higher than marginal R^2 value (0.103). After controlling for significant variation explained by age (Estimate = 0.056, *SE* = 0.017, *P* = 0.002; Table 2 and Figure 2C) and body mass (Estimate = -0.047, *SE* = 0.020, *P* = 0.020; Table 2 and Figure 2D), the N/L ratio had a nonsignificant trend to decrease with relative rank (Estimate = -0.026, *SE* = 0.015, *P* = 0.076; Table 2 and Figure 2A). Rather, whereas this pattern was not statistically significant, male marmots that have relatively higher dominance rank tended to show lower value of N/L ratio (Figure 2A). Therefore, whereas older males had lower immune status (Figure 2C,D), higher-ranking and heavier males tended to have higher

Table 2. Independent variables explaining variation in neutrophil to lymphocyte ratios in adult male yellow-bellied marmots

Fixed effects:	Estimate	<i>SE</i>	<i>df</i>	<i>t</i> value	<i>P</i> -value
(Intercept)	0.234	0.032	11.204	7.320	<0.001
Social rank	-0.026	0.015	74.174	-1.798	0.076
FCM levels	-0.012	0.017	63.824	-0.696	0.489
Age	0.056	0.017	55.705	3.277	0.002
Body mass	-0.047	0.020	95.871	-2.365	0.020
Day of year	0.009	0.019	102.721	0.440	0.661
	Conditional R^2		Marginal R^2		
	0.103		0.466		
Random effects:	Variance	SD			
Individual ID	(Intercept)	<0.001	0.018	—	—
Year	(Intercept)	0.011	0.105	—	—
Colony ID	(Intercept)	0.000	0.021	—	—
Residual		0.017	0.132	—	—

Conditional and marginal R^2 are shown. Significant values in bold.

immune status (Figure 2A,D). This finding is consistent with the prediction of the resource quality hypothesis. There was no significant association between FCM levels and N/L ratios (Estimate = -0.012, *SE* = 0.017, *P* = 0.489; Table 2 and Figure 2B).

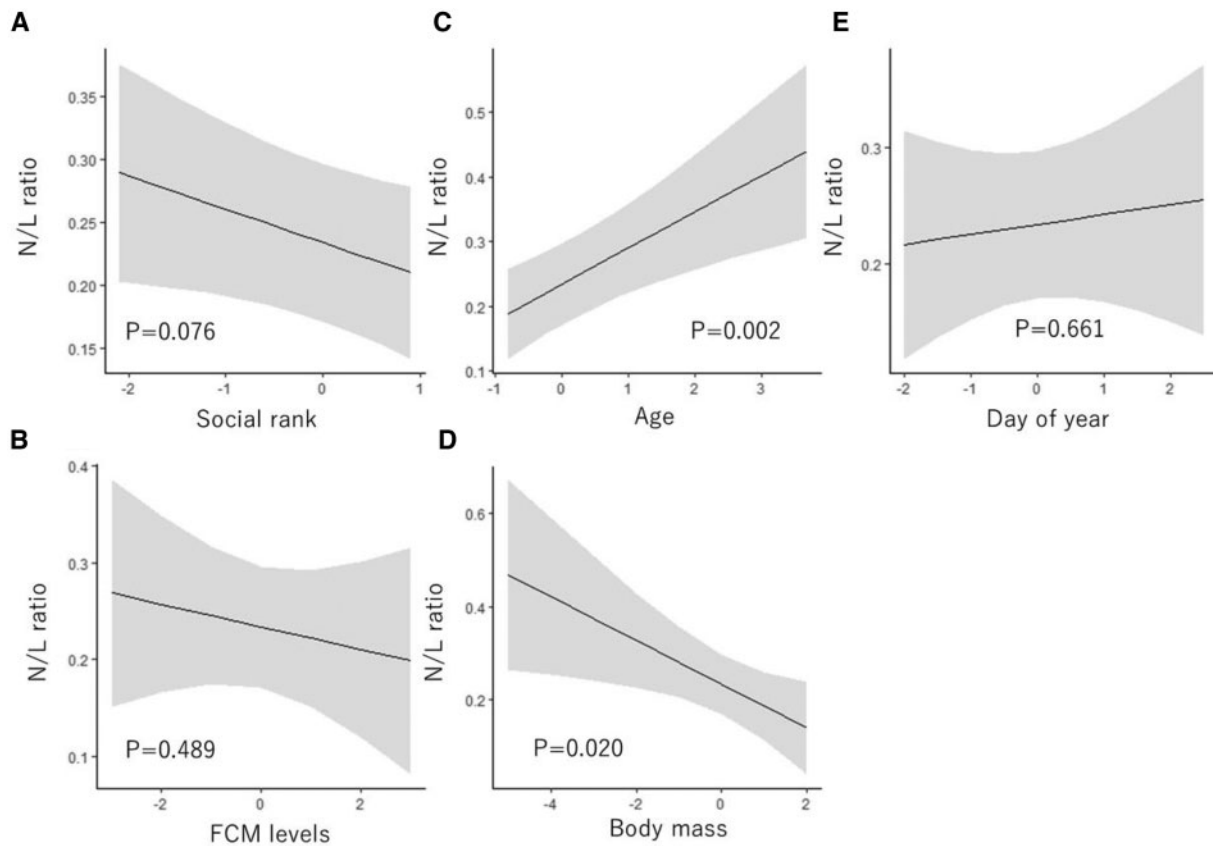


Figure 2. The relationships between standardized fixed effects (A) social rank, (B) FCM levels, (C) age, (D) body mass, and (E) day of year and log-transformed N/L ratios. Each line was calculated using the predicted probabilities from the LMM (see text for details). Buffers represent the 95% confidence interval. *P*-values are reported from the LMM.

Discussion

We examined the relationship between dominance rank and 2 health-related factors, FCM levels and N/L ratios, which were indices of physiological stress and immunocompetence, respectively, in adult male yellow-bellied marmots. We found that higher-ranking individuals tended to have lower N/L ratios compared with subordinate individuals, and that N/L ratios decreased with body mass (a correlate of dominance rank). Additionally, male FCM levels were associated with neither social rank nor body mass. We also found no relationship between FCM levels and N/L ratios. Although we did not experimentally test the immunocompetence handicap hypothesis, our results tend to show that health of high-ranking males may not be impaired compared with subordinate individuals. Instead, our findings suggest that high-ranking male marmots are able to buffer the energetic costs of reproduction and competition, possibly because of better access to resources. Our results are also consistent with current findings in a number of wild animals, as well as humans, that show enhanced health outcomes in individuals of higher social rank (Snyder-Mackler et al. 2020).

The cost of maintaining high social status is a key assumption of the immunocompetence handicap hypothesis, and we, therefore, predicted that males with higher social rank would exhibit lower health, indicated by higher FCM levels and N/L ratios. Instead, our results showed the opposite relationship (for N/L ratios), or no relationship (for FCMs). These observations are consistent with previous studies that found no significant relationships between social

rank and immunological status (Webster et al. 2018), and some have found the better health conditions in higher-ranking individuals (Gesquiere et al. 2011; Archie et al. 2014).

In short, these results are more consistent with the resource quality hypothesis which predicts good health conditions in dominant individuals due to their priority access to resources. This hypothesis also predicts that although resource quality directly influences an individual's immune status, they also indirectly effect immune status via enhancing body condition (Diamond and Kingsolver 2011). In our case, higher-ranking male marmots may have priority access to resources and this may explain why measures of FCM levels did not increase with rank, whereas N/L ratios tended to decrease with rank, as seen in other species (Lindström 2004; Flies et al. 2016). Additionally, dominant male marmots tend to be in better body conditions than subordinates (Huang et al. 2011) and we now know that N/L ratios decreased with body mass. Having sufficient body mass to survive hibernation is essential (Armitage 2014), and low-body mass individuals may be immunologically compromised as seen by their tendency to have enhanced N/L ratios. In a variety of species, high N/L ratios are also associated with poor future health outcomes that may include increased pathogen or parasite infections, cardiovascular risk, slower growth, and reduced survival (Moreno et al. 2002; Horne et al. 2005; Kilgas et al. 2006). This could suggest reduced survival of subordinate marmots, which would need to be empirically examined in future studies to improve our understanding of the fitness consequences of dominance status.

We have known that higher-ranking male marmots have higher reproductive success (Huang et al. 2011), and we now know that dominant males tend to be in better immunological condition, at least as measured using N/L ratios, whereas there is no significant relationship between dominance rank and GC levels. Taken together, these results suggest that being socially dominant may not have substantial costs in terms of health, and could even provide health benefits and ultimately is associated with higher male reproductive success.

The relationship between social status and the endocrine and immune systems is often species-specific (Roberts et al. 2004). Much previous work looking at this nexus has focused on animals living in the laboratory (Roberts et al. 2004) as well as on free-living primates (Gesquiere et al. 2011), and other highly social species (Flies et al. 2016; Smyth et al. 2018). The lack of the relationship between social status and FCM levels and the modest effect size of dominance on N/L ratios in our study differs from previous studies of free-living, obligately social mammals such as wolves (*Canis lupus*; Sands and Creel 2004), meerkats (Smyth et al. 2018), and some primates (Muller and Wrangham 2004; Archie et al. 2012) in which individual health levels either significantly increased or decreased with social rank.

Because the nature of social dominance varies among species and is influenced by a variety of life-history characteristics, our findings may in part be explained by the social structure of yellow-bellied marmots. Variation in sociality in facultatively social species is influenced by many factors, and we might assume that individuals are found in groups when the benefits exceed the costs of sociality (Alexander 1974). The flexible life-history strategy of yellow-bellied marmots may buffer any relationships between social status and immune functions in adult males. Differences across field studies might also reflect the way in which immunocompetence was measured. Although many studies have used N/L ratios, some studies have also employed other tests such as bacteria-killing, hemolytic complement, and an immunoglobulin G assay (Liebl and Martin 2009; Flies et al. 2016). Although these measurements address, in a broad sense, immunity, the underlying mechanisms are slightly different. Additionally, for field studies of free-living animals, other factors such as a variety of seasonal, diurnal, and environmental factors (Wingfield 2005) may be relatively more important than social status on immunological condition in a facultatively social species. Our results suggest that much is to be gained by studying other free-living species, particularly those that are not obligately social.

Older male marmots are typically socially dominant to younger males (Huang et al. 2011). Therefore, we might expect that FCM levels would increase with age under the immunocompetence handicap hypothesis. However, we found the opposite. Younger adult males that recently immigrated to a colony may still be adjusting to life and most likely encounter more stressful circumstances than those of older, more socially stable marmots (Armitage 1991). Seasonal growth was significantly associated with survival in yearling marmots compared with adult conspecifics, resulting in higher costs of growth in young marmots (Heissenberger et al. 2020). These age-related costs would directly influence FCM levels rather than interacting with social status in male marmots.

Physiological stress levels may vary seasonally as has been seen in other hibernating animals (e.g., Reeder et al. 2004). However, it was reported that GCs were highest before the hibernation season began (Reeder et al. 2004), whereas here we found the opposite. This might be attributed to the fact that the frequency of socially stressful activities, such as male–male competition, is likely to be higher in the early season than later in the season where marmot social activity declines.

We acknowledge that although we examined the correlation between dominance rank and health conditions, we did not rigorously test the immunocompetence handicap hypothesis by carrying out experimental manipulations, which are, ultimately, required (Getty 2002). Manipulating dominance in our free-living system would be difficult, but perhaps manipulating parasite loads and studying immunological consequences could be revealed in future studies.

Immunological performance is known to decrease with age as a result of immunosenescence (Bosch et al. 2013; Neggazi et al. 2016; Carillet et al. 2019). For example, Van Lieshout et al. (2020) found that the proportion of lymphocytes declined with age in European badgers (*Meles meles*). Our study also found that older male marmots have higher N/L ratios. Because there was no significant effect of the interaction between social rank and age in our study, the effect of age may be directly associated with the immunity of male marmots.

In conclusion, we found increased immune function with social rank in yellow-bellied marmots, which is consistent with the resource quality hypothesis. In male marmots, achieving and maintaining high social status is not obviously costly, suggesting that dominance not only has benefits in terms of reproductive success, but benefits also in terms of increased health status. Because testosterone plays a key role in the underlying mechanisms of relationships between male reproductive behaviors and immune function, future studies directly studying the role that testosterone plays in maintaining dominance would help further understand these results. And, because females also maintain dominant hierarchies, future studies of the relationship between rank and female health are warranted.

Acknowledgments

We are grateful to all marmoteers who collected data over many years, and the RMBL which has helped facilitate this research, and the 2 reviewers for their very constructive comments. All procedures were approved under research protocol ARC 2001-191-01 by the University of California Los Angeles Animal Care Committee on 13 May 2002, and renewed annually, as well as annual permits issued by the Colorado Division of Wildlife (TR-519).

Funding

K.U. was supported by the Japan Society for the Promotion of Science Overseas Research Fellowship. J.E.S. was supported by the American Association of University Women, Institute for Society and Genetics at the University of California Los Angeles, and American Philosophical Society for fellowships. D.T.B. was supported by the National Geographic Society, UCLA (Faculty Senate and the Division of Life Sciences), a Rocky Mountain Biological Laboratory research fellowship, and by the National Science Foundation (I.D.B.R.-0754247, and D.E.B.-1119660 and 1557130 to D.T.B., as well as D.B.I. 0242960, 0731346, and 1226713 RMBL).

Supplementary Material

Supplementary material can be found at <https://academic.oup.com/cz>.

Conflict of Interest

The authors report no conflicts of interest.

Data Availability Statement

Code and data will be made available on Open Science Framework (OSF) following acceptance.

References

- Alexander RD, 1974. The evolution of social behavior. *Annu Rev Ecol Syst* 5: 325–383.
- Archie EA, Altmann J, Alberts SC, 2012. Social status predicts wound healing in wild baboons. *Proc Natl Acad Sci USA* 109:9017–9022.
- Archie EA, Altmann J, Alberts SC, 2014. Costs of reproduction in a long-lived female primate: injury risk and wound healing. *Behav Ecol Sociobiol* 68: 1183–1193.
- Armitage KB, 1991. Social and population dynamics of yellow-bellied marmots: results from long-term research. *Annu Rev Ecol Syst* 22:379–407.
- Armitage KB, 2014. *Marmot Biology: Sociality, Individual Fitness and Population Dynamics*. Cambridge: Cambridge University Press.
- Barto K, 2020. MuMIn: multi-model inference. R package version 1.43.17. Available from: <https://CRAN.R-project.org/package=MuMIn> (accessed 21 April 2021).
- Bates D, Mächler M, Bolker B, Walker S, 2015. Fitting linear mixed-effects models using lme4. *J Stat Softw* 67:1–48.
- Blumstein DT, 2013. Yellow-bellied marmots: insights from an emergent view of sociality. *Philos Trans R Soc B Biol Sci* 368:20120349.
- Blumstein DT, Chung LK, Smith JE, 2013. Early play may predict later dominance relationships in yellow-bellied marmots *Marmota flaviventris*. *Proc Roy Soc B* 280:20130485.
- Blumstein DT, Keeley KN, Smith J, 2016. Fitness and hormonal correlates of social and ecological stressors of female yellow-bellied marmots. *Anim Behav* 112:1–11.
- Blumstein DT, Patton ML, Saltzman W, 2006. Faecal glucocorticoid metabolites and alarm calling in free-living yellow-bellied marmots. *Biol Lett* 2: 29–32.
- Blumstein DT, Wey TW, Tang K, 2009. A test of the social cohesion hypothesis: Interactive female marmots remain at home. *Proceedings Series B* 276: 3007–3012.
- Bosch JA, Phillips AC, Lord JM, 2013. *Immunosenescence: Psychosocial and Behavioral Differences*. 1st edn. New York (NY): Springer, Bücher.
- Carbillet J, Rey B, Lavabre T, Chaval Y, Merlet J et al., 2019. The neutrophil to lymphocyte ratio indexes individual variation in the behavioural stress response of wild roe deer across fluctuating environmental conditions. *Behav Ecol Sociobiol* 73:114.
- Clutton-Brock TH, Albon SD, Gibson RM, Guinness FE, 1972. The logical stag: adaptive aspects of fighting in red deer (*Cervus elaphus* L.). *Anim Behav* 27:211–225.
- Davis AK, Maney DL, Maerz JC, 2008. The use of leukocyte profiles to measure stress in vertebrates: a review for ecologists. *Funct Ecol* 22:760–772.
- Diamond SE, Kingsolver JG, 2011. Host plant quality, selection history and trade-offs shape the immune responses of *Manduca sexta*. *Proc R Soc B Biol Sci* 278:289–297.
- Fabiani A, Galimberti F, Sanvito S, Hoelzel AR, 2004. Extreme polygyny among southern elephant seals on Sea Lion Island, Falkland Islands. *Behav Ecol* 15:961–969.
- Flies AS, Mansfield LS, Flies EJ, Grant CK, Holekamp KE, 2016. Socioecological predictors of immune defences in wild spotted hyenas. *Funct Ecol* 30:1549–1557.
- Folstad I, Karter AJ, 1992. Parasites, bright males, and the immunocompetence handicap. *Am Nat* 139:603–622.
- Fox J, Weisberg S, 2018. *An R Companion to Applied Regression*. Thousand Oaks (CA): Sage Publications.
- Gesquiere LR, Learn NH, Simao MCM, Onyango PO, Alberts SC et al., 2011. Life at the top: rank and stress in wild male baboons. *Science* 333:357–360.
- Getty T, 2002. Signaling health versus parasites. *Am Nat* 159:363–371.
- Gormally BMG, Romero LM, 2020. What are you actually measuring? A review of techniques that integrate the stress response on distinct time-scales. *Funct Ecol* 34:2030–2044.
- Goymann W, Moore IT, Scheuerlein A, Hirschenhauser K, Grafen A et al., 2004. Testosterone in tropical birds: effects of environmental and social factors. *Am Nat* 164:327–334.
- Hadinger U, Haymerle A, Knauer F, Schwarzenberger F, Walzer C, 2015. Faecal cortisol metabolites to assess stress in wildlife: evaluation of a field method in free-ranging chamois. *Methods Ecol Evol* 6:1349–1357.
- Heissenberger S, de Pinho GM, Martin JG, Blumstein DT, 2020. Age and location influence the costs of compensatory and accelerated growth in a hibernating mammal. *Behav Ecol* 31:826–833.
- Holding ML, Putman BJ, Kong LM, Smith JE, Clark RW, 2020. Physiological stress integrates resistance to rattlesnake venom and the onset of risky foraging in California ground squirrels. *Toxins* 12:617.
- von Holst D, Hutzelmeyer H, Kaetzke P, Khaschei M, Schönheiter R, 1999. Social rank, stress, fitness, and life expectancy in wild rabbits. *Naturwissenschaften* 86:388–393.
- Hoogland JL, Foltz DW, 1982. Variance in male and female reproductive success in a harem-polygynous mammal, the black-tailed prairie dog (Sciuridae: *Cynomys ludovicianus*). *Behav Ecol Sociobiol* 11:155–163.
- Horne BD, Anderson JL, John JM, Weaver A, Bair TL et al., 2005. Which white blood cell subtypes predict increased cardiovascular risk? *J Am Coll Cardiol* 45:1638–1643.
- Huang B, Wey TW, Blumstein DT, 2011. Correlates and consequences of dominance in a social rodent. *Ethology* 117:573–585.
- Johnstone CP, Reina RD, Lill A, 2012. Interpreting indices of physiological stress in free-living vertebrates. *J Comp Physiol B Biochem Syst Environ Physiol* 182:861–879.
- Kilgas P, Tilgar V, Mänd R, 2006. Hematological health state indices predict local survival in a small passerine bird, the great tit *Parus major*. *Physiol Biochem Zool* 79:565–572.
- Kuznetsova A, Brockhoff PB, Christensen RHB, 2017. lmerTest package: tests in linear mixed effects models. *J Stat Softw* 82:1–26.
- Levy EJ, Gesquiere LR, McLean E, Franz M, Warutere JK et al., 2020. Higher dominance rank is associated with lower glucocorticoids in wild female baboons: a rank metric comparison. *Horm Behav* 125:104826.
- Liebl AL, Martin Li LB, 2009. Simple quantification of blood and plasma antimicrobial capacity using spectrophotometry. *Funct Ecol* 23:1091–1096.
- Van Lieshout SHJ, Badás EP, Mason MWT, Newman C, Buesching CD et al., 2020. Social effects on age-related and sex-specific immune cell profiles in a wild mammal. *Biol Lett* 16:20200234.
- Lindström KM, 2004. Social status in relation to Sindbis virus infection clearance in greenfinches. *Behav Ecol Sociobiol* 55:236–241.
- Martin LB, 2009. Stress and immunity in wild vertebrates: timing is everything. *Gen Comp Endocrinol* 163:70–76.
- Martin PR, Bateson P, 1993. *Measuring Behaviour: An Introductory Guide*. Cambridge: Cambridge University Press.
- Montgomery TM, Pendleton EL, Smith JE, 2018. Physiological mechanisms mediating patterns of reproductive suppression and alloparental care in cooperatively breeding carnivores. *Physiol Behav* 193:167–178.
- Moreno J, Merino S, Martínez J, Sanz JJ, Arriero E, 2002. Heterophil/lymphocyte ratios and heat-shock protein levels are related to growth in nestling birds. *Écoscience* 9:434–439.
- Mougeot F, Redpath SM, Piertney SB, 2006. Elevated spring testosterone increases parasite intensity in male red grouse. *Behav Ecol* 17:117–125.
- Muller MN, Wrangham RW, 2004. Dominance, cortisol and stress in wild chimpanzees *Pan troglodytes schweinfurthii*. *Behav Ecol Sociobiol* 55: 332–340.
- Nakagawa S, Schielzeth H, 2013. A general and simple method for obtaining R² from generalized linear mixed-effects models. *Methods Ecol Evol* 4: 133–142.
- Neggazi SA, Noreikiene K, Öst M, Jaatinen K, 2016. Reproductive investment is connected to innate immunity in a long-lived animal. *Oecologia* 182: 347–356.
- Osorno JL, Núñez-de la-Mora A, D’Alba L, Wingfield JC, 2010. Hormonal correlates of breeding behavior and pouch color in the magnificent frigatebird *Fregata magnificens*. *Gen Comp Endocrinol* 169:18–22.
- Pride RE, 2005. High faecal glucocorticoid levels predict mortality in ring-tailed lemurs *Lemur catta*. *Biol Lett* 1:60–63.
- R Core Team. 2020. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. Available from: <https://www.R-project.org/>.
- Réale D, Garant D, Humphries MM, Bergeron P, Careau V et al., 2010. Personality and the emergence of the pace-of-life syndrome concept at the population level. *Philos Trans R Soc B* 365:4051–4063.

- Reeder DAM, Kosteczko NS, Kunz TH, Widmaier EP, 2004. Changes in baseline and stress-induced glucocorticoid levels during the active period in free-ranging male and female little brown myotis *Myotis lucifugus* (Chiroptera: Vespertilionidae). *Gen Comp Endocrinol* 136:260–269.
- Roberts ML, Buchanan KL, Evans MR, 2004. Testing the immunocompetence handicap hypothesis: a review of the evidence. *Anim Behav* 68:227–239.
- Salvador A, Veiga JP, Martin J, Lopez P, Abellanda M et al., 1996. The cost of producing a sexual signal: testosterone increases the susceptibility of male lizards to ectoparasitic infestation. *Behav Ecol* 7:145–150.
- Sands J, Creel S, 2004. Social dominance, aggression and faecal glucocorticoid levels in a wild population of wolves, *Canis lupus*. *Anim Behav* 67:387–396.
- Sapolsky RM, 2005. The influence of social hierarchy on primate health. *Science* 308:648–652.
- Sapolsky RM, Romero LM, Munck AU, 2000. How do glucocorticoids influence stress responses? Integrating permissive, suppressive, stimulatory, and preparative actions. *Endocr Rev* 21:55–89.
- Smith JE, Chung LK, Blumstein DT, 2013. Ontogeny and symmetry of social partner choice among free-living yellow-bellied marmots. *Anim Behav* 85:715–725.
- Smith JE, Monclús R, Wantuck D, Florant GL, Blumstein DT, 2012. Fecal glucocorticoid metabolites in wild yellow-bellied marmots: experimental validation, individual differences and ecological correlates. *Gen Comp Endocrinol* 178:417–426.
- Smyth KN, Caruso NM, Davies CS, Clutton-Brock TH, Drea CM, 2018. Social and endocrine correlates of immune function in meerkats: implications for the immunocompetence handicap hypothesis. *R Soc Open Sci* 5:180435.
- Snyder-Mackler N, Burger JR, Gaydos L, Belsky DW, Noppert GA et al., 2020. Social determinants of health and survival in humans and other animals. *Science* 368:eaax9553.
- Trivers RL, 1972. Parental investment and sexual selection. In: Campbell B, editor. *Sexual Selection and the Descent of Man*. Chicago: Aldine. 136–179.
- Wasser SK, Hunt KE, Brown JL, Cooper K, Crockett CM et al., 2000. A generalized fecal glucocorticoid assay for use in a diverse array of nondomestic mammalian and avian species. *Gen Comp Endocrinol* 120:260–275.
- Webster MS, Ligon RA, Leighton GM, 2018. Social costs are an underappreciated force for honest signalling in animal aggregations. *Anim Behav* 143:167–176.
- Wey TW, Blumstein DT, 2010. Social cohesion in yellow-bellied marmots is established through age and kin structuring. *Anim Behav* 79:1343–1352.
- Wingfield JC, 2005. The concept of allostasis: coping with a capricious environment. *J Mammal* 86:248–254.