Trophy hunters pay more to target larger-bodied carnivores

Ilona Mihalik, Andrew W. Bateman and Chris T. Darimont

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Original submission: 18 December 2018
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2nd revised submission: 12 August 2019
Final acceptance: 13 August 2019

Note: Reports are unedited and appear as submitted by the referee. The review history appears in chronological order.

Review History

RSOS-182113.R0 (Original submission)

Review form: Reviewer 1 (Christopher R. von Rueden)

Is the manuscript scientifically sound in its present form?
Yes

Are the interpretations and conclusions justified by the results?
No

Is the language acceptable?
Yes

Is it clear how to access all supporting data?
Yes

Do you have any ethical concerns with this paper?
No

Have you any concerns about statistical analyses in this paper?
No
Recommendation?
Reject

Comments to the Author(s)
The authors look at prices of trophy hunts in North America to test a signaling theory of hunters’ motivations. While there is great potential benefit here to inform conservation policy, I have some issues with application of signaling theory to this dataset. First, there is no determination of what hunters are signaling by targeting game that is rare, dangerous, etc. Second, paying more to go on a hunt does not clearly signal any underlying quality on part of these hunters, such as physical condition or intelligence. It may be that those with more money can afford such hunts, but it’s unlikely the hunts are primarily responsible for indicating affluence of the hunters to their peers. A reputation model and not a costly signaling model per se may be the better theoretical approach. These theoretical concerns don’t aid the largely null results, which add to our inability to take much from the paper. I elaborate on these comments below.

Page 3, Line 28: the behavior you describe (paying large fees and traveling to unfamiliar areas) is clearly not the aspects of the behavior that evolved. Targeting large individuals and rare taxa may be (as you describe at the beginning of the paragraph) but your references are for modern trophy hunting not archaeological or ethnographic evidence from foragers. You should cite evidence here that such hunting behavior is characteristic of humans beyond modern trophy hunting. The Foraging Spectrum book by Kelly is a good overview. As well as studies you cite later, from Hawkes, Bliege Bird, etc.

Page 3, Line 52: Costly signaling means signalers must pay an extra cost (the handicap) at equilibrium, and high quality signalers can better afford this marginal cost. So its not that only certain individuals can pay the cost- its that certain individuals can better afford the marginal cost.

Page 4, Line 26: say what you mean by the theory not being universally accepted, per the article you cite. I think the gist is that signals need not be costly to be honest. Rather, the potential cost of cheating can keep signals honest, or some signals can be difficult if not impossible to fake (i.e. indices), or honest signalers may benefit more than fakers. Can these possibilities explain hunting behavior? Comment on this.

Page 5, Line 5: in traditional societies, there is typically a substantial fraction of hunted game that is kept by hunters and given to their families (see work by Michael Gurven). Thus hunting is unlikely to be purely or even principally a costly signal, or one that is “wasteful”. Indeed, much of the higher reproductive success attributable to better hunters may flow through family provisioning. See Gurven and von Rueden “Hunting social status and biological fitness”. Also see paper by Wood and Marlowe “Household and kin provisioning by Hadza men” that shows Hadza hunters target both small and large game and game of all sizes is widely shared. Hunting motivations are multi-faceted.

Page 5, Line 15: What is hunting actually signaling that begets higher reproductive success? There is no good evidence of this. The authors you cite only speculate, so be clear on this. An alternative to the costly signaling account of hunting is a reputation account. For details see “Costly signaling and the handicap principle in anthropology and zoology: a review” by Duncan Stibbard-Hawkes. It also makes points similar to comments above.

Page 5, Line 45: In the context of modern trophy hunting, affluence is unlikely to be signaled principally by killing particular prey. Taking the hunting trip itself is an indication of affluence, and those spending a lot on hunting are also likely to spend a lot on other material goods, e.g. billionaires who trophy hunt the African Big Five. Also, physical competency and cognitive ability are not necessarily required when guides and vehicles and sophisticated weaponry are on hand- as you recognize.

Page 6, Line 22: status among whom? Among Safari Club members, but normative disapproval of trophy hunting (e.g. Cecil the Lion) suggests status benefits are not likely to be widespread.
Page 6, Line 29: I suggest you set up an alternative prediction, that rarity associates with higher price because of supply/demand based on quotas to conserve the population. And this rarity need not be primarily a consequence of the Anthropogenic Allee Effect. But you wouldn’t predict such quotas would track body size, danger, difficulty to hunt, or carnivory per se (independent of rarity).

Page 17, Line 17: Investigating the motives of trophy hunters is important for conservation efforts, perhaps particularly so in North America, but in many parts of the world subsistence hunting has bigger consequences for endangered wildlife. To what extent does trophy hunting provide benefits for conservation, e.g. revenue is funneled into wildlife education or protected area management or lobbying.

Review form: Reviewer 2

Is the manuscript scientifically sound in its present form?  
Yes

Are the interpretations and conclusions justified by the results?  
Yes

Is the language acceptable?  
Yes

Is it clear how to access all supporting data?  
Yes

Do you have any ethical concerns with this paper?  
No

Have you any concerns about statistical analyses in this paper?  
I do not feel qualified to assess the statistics

Recommendation?  
Accept with minor revision (please list in comments)

Comments to the Author(s)  
This is an interesting manuscript that makes a modest but solid contribution to the literatures on human signaling and commercial big game hunting.

My only problem with the manuscript is with the authors’ presentation of costly signaling theory. They seem to equate costly signals with handicaps. That is not correct. One way to make a signal costly, and thus more likely to overcome a receiver's skepticism regarding the accuracy of the information it is trying to convey, is to make it a handicap. But that's not the only way to do it, and I don't think paying a lot of money to kill a bear or an elk qualifies as a handicap. I recommend the authors re-read the Grose article that they already cite. These two citations might also be useful:

Cronk, L., 2005. The application of animal signaling theory to human phenomena: some thoughts and clarifications. Social Science Information, 44(4), pp.603-620.

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Regarding the Grose article, I think his problem is not so much with costly signaling theory in general, as implied by the way the authors of this manuscript cite it, but rather with how the handicap principle has been applied or misapplied.

Finally, I agree that the example of turtle hunting by the Meriam is a good one to use. The following article makes the same kind of point based on data from another island society, so the authors might want to cite it, as well:

Sosis, R., 2000. Costly signaling and torch fishing on Ifaluk Atoll. Evolution and Human Behavior, 21(4), pp.223-244.

Decision letter (RSOS-182113.R0)

20-Feb-2019

Dear Ms Mihalik:

Manuscript ID RSOS-182113 entitled "Big game hunters pay more to target larger-bodied carnivores: insight from costly signalling theory" which you submitted to Royal Society Open Science, has been reviewed. The comments from reviewers are included at the bottom of this letter.

In view of the criticisms of the reviewers, the manuscript has been rejected in its current form. However, a new manuscript may be submitted which takes into consideration these comments.

Please note that resubmitting your manuscript does not guarantee eventual acceptance, and that your resubmission will be subject to peer review before a decision is made.

You will be unable to make your revisions on the originally submitted version of your manuscript. Instead, revise your manuscript and upload the files via your author centre.

Once you have revised your manuscript, go to https://mc.manuscriptcentral.com/rsos and login to your Author Center. Click on "Manuscripts with Decisions," and then click on "Create a Resubmission" located next to the manuscript number. Then, follow the steps for resubmitting your manuscript.

Your resubmitted manuscript should be submitted by 20-Aug-2019. If you are unable to submit by this date please contact the Editorial Office.

We look forward to receiving your resubmission.

Kind regards,
Andrew Dunn
Royal Society Open Science Editorial Office
Royal Society Open Science
openscience@royalsociety.org

on behalf of Dr Claudia Wascher (Associate Editor) and Kevin Padian (Subject Editor)
openscience@royalsociety.org
The presented manuscript aims at testing whether predictions derived from costly signalling theory would apply to modern day big game hunting in humans and investigated whether the price to hunt a specific species would depend on the rarity, danger, or difficulty imposed by the species. The authors did find body size to positively affect hunting price. Both reviewers find the contribution potentially interesting, but raise concerns regarding the general framing of the manuscript within signalling theory. These concerns need to be addressed prior to potential publication of the manuscript.

I agree that the results of this manuscript will be of great interest to conservationists (and I think will raise awareness among the general public). However, there are concerns about framing this within the general theory of costly signaling, and reviewers and editors think that this needs some rethinking. If you choose to resubmit, please address these concerns fully in your response. Thanks for submitting.

The authors look at prices of trophy hunts in North America to test a signaling theory of hunters’ motivations. While there is great potential benefit here to inform conservation policy, I have some issues with application of signaling theory to this dataset. First, there is no determination of what hunters are signaling by targeting game that is rare, dangerous, etc. Second, paying more to go on a hunt does not clearly signal any underlying quality on part of these hunters, such as physical condition or intelligence. It may be that those with more money can afford such hunts, but it's unlikely the hunts are primarily responsible for indicating affluence of the hunters to their peers. A reputation model and not a costly signaling model per se may be the better theoretical approach. These theoretical concerns don’t aid the largely null results, which add to our inability to take much from the paper. I elaborate on these comments below.

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Reviewer: 2

Comments to the Author(s)

This is an interesting manuscript that makes a modest but solid contribution to the literatures on human signaling and commercial big game hunting.

My only problem with the manuscript is with the authors’ presentation of costly signaling theory. They seem to equate costly signals with handicaps. That is not correct. One way to make a signal costly, and thus more likely to overcome a receiver’s skepticism regarding the accuracy of the information it is trying to convey, is to make it a handicap. But that's not the only way to do it, and I don't think paying a lot of money to kill a bear or an elk qualifies as a handicap. I recommend the authors re-read the Grose article that they already cite. These two citations might also be useful:

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Sosis, R., 2000. Costly signaling and torch fishing on Ifaluk Atoll. Evolution and Human Behavior, 21(4), pp.223-244.

Author's Response to Decision Letter for (RSOS-182113.R0)

See Appendix A.

RSOS-191231.R0

Review form: Reviewer 1 (Christopher R. von Rueden)

Is the manuscript scientifically sound in its present form?
Yes

Are the interpretations and conclusions justified by the results?
Yes

Is the language acceptable?
Yes

Do you have any ethical concerns with this paper?
No

Have you any concerns about statistical analyses in this paper?
No

Recommendation?
Accept as is

Comments to the Author(s)
The changes addressed my concerns- looks good.
Review form: Reviewer 2

Is the manuscript scientifically sound in its present form?
Yes

Are the interpretations and conclusions justified by the results?
Yes

Is the language acceptable?
Yes

Do you have any ethical concerns with this paper?
No

Have you any concerns about statistical analyses in this paper?
No

Recommendation?
Accept as is

Comments to the Author(s)
The authors have taken the reviewers' comments to heart and greatly clarified their manuscript. The distinction between "cost" and "price" is especially helpful.

The only change I would recommend is the deletion of the subtitle. I does not seem necessary. The title alone summarizes the manuscript's main finding.

Decision letter (RSOS-191231.R0)

29-Jul-2019

Dear Ms Mihalik

On behalf of the Editor, I am pleased to inform you that your Manuscript RSOS-191231 entitled "Big game hunters pay more to target larger-bodied carnivores: money, guns, and costly signals in non-subsistence systems" has been accepted for publication in Royal Society Open Science subject to minor revision in accordance with the referee suggestions. Please find the referees' comments at the end of this email.

The reviewers and Subject Editor have recommended publication, but also suggest some minor revisions to your manuscript. Therefore, I invite you to respond to the comments and revise your manuscript.

• Ethics statement
If your study uses humans or animals please include details of the ethical approval received, including the name of the committee that granted approval. For human studies please also detail whether informed consent was obtained. For field studies on animals please include details of all permissions, licences and/or approvals granted to carry out the fieldwork.
• Data accessibility
It is a condition of publication that all supporting data are made available either as supplementary information or preferably in a suitable permanent repository. The data accessibility section should state where the article's supporting data can be accessed. This section should also include details, where possible of where to access other relevant research materials such as statistical tools, protocols, software etc can be accessed. If the data has been deposited in an external repository this section should list the database, accession number and link to the DOI for all data from the article that has been made publicly available. Data sets that have been deposited in an external repository and have a DOI should also be appropriately cited in the manuscript and included in the reference list.

If you wish to submit your supporting data or code to Dryad (http://datadryad.org/), or modify your current submission to dryad, please use the following link: http://datadryad.org/submit?journalID=RSOS&manu=RSOS-191231

• Competing interests
Please declare any financial or non-financial competing interests, or state that you have no competing interests.

• Authors’ contributions
All submissions, other than those with a single author, must include an Authors’ Contributions section which individually lists the specific contribution of each author. The list of Authors should meet all of the following criteria; 1) substantial contributions to conception and design, or acquisition of data, or analysis and interpretation of data; 2) drafting the article or revising it critically for important intellectual content; and 3) final approval of the version to be published.

All contributors who do not meet all of these criteria should be included in the acknowledgements.

We suggest the following format:
AB carried out the molecular lab work, participated in data analysis, carried out sequence alignments, participated in the design of the study and drafted the manuscript; CD carried out the statistical analyses; EF collected field data; GH conceived of the study, designed the study, coordinated the study and helped draft the manuscript. All authors gave final approval for publication.

• Acknowledgements
Please acknowledge anyone who contributed to the study but did not meet the authorship criteria.

• Funding statement
Please list the source of funding for each author.

Please note that we cannot publish your manuscript without these end statements included. We have included a screenshot example of the end statements for reference. If you feel that a given heading is not relevant to your paper, please nevertheless include the heading and explicitly state that it is not relevant to your work.

Because the schedule for publication is very tight, it is a condition of publication that you submit the revised version of your manuscript before 07-Aug-2019. Please note that the revision deadline will expire at 00.00am on this date. If you do not think you will be able to meet this date please let me know immediately.
To revise your manuscript, log into https://mc.manuscriptcentral.com/rsos and enter your Author Centre, where you will find your manuscript title listed under "Manuscripts with Decisions". Under "Actions," click on "Create a Revision." You will be unable to make your revisions on the originally submitted version of the manuscript. Instead, revise your manuscript and upload a new version through your Author Centre.

When submitting your revised manuscript, you will be able to respond to the comments made by the referees and upload a file "Response to Referees" in "Section 6 - File Upload". You can use this to document any changes you make to the original manuscript. In order to expedite the processing of the revised manuscript, please be as specific as possible in your response to the referees.

When uploading your revised files please make sure that you have:

1) A text file of the manuscript (tex, txt, rtf, docx or doc), references, tables (including captions) and figure captions. Do not upload a PDF as your "Main Document".
2) A separate electronic file of each figure (EPS or print-quality PDF preferred (either format should be produced directly from original creation package), or original software format)
3) Included a 100 word media summary of your paper when requested at submission. Please ensure you have entered correct contact details (email, institution and telephone) in your user account
4) Included the raw data to support the claims made in your paper. You can either include your data as electronic supplementary material or upload to a repository and include the relevant doi within your manuscript
5) All supplementary materials accompanying an accepted article will be treated as in their final form. Note that the Royal Society will neither edit nor typeset supplementary material and it will be hosted as provided. Please ensure that the supplementary material includes the paper details where possible (authors, article title, journal name).

Supplementary files will be published alongside the paper on the journal website and posted on the online figshare repository (https://figshare.com). The heading and legend provided for each supplementary file during the submission process will be used to create the figshare page, so please ensure these are accurate and informative so that your files can be found in searches. Files on figshare will be made available approximately one week before the accompanying article so that the supplementary material can be attributed a unique DOI.

Once again, thank you for submitting your manuscript to Royal Society Open Science and I look forward to receiving your revision. If you have any questions at all, please do not hesitate to get in touch.

Kind regards,
Alice Power
Editorial Coordinator
Royal Society Open Science
openscience@royalsociety.org

on behalf of Dr Claudia Wascher (Associate Editor) and Kevin Padian (Subject Editor)
openscience@royalsociety.org
Associate Editor Comments to Author (Dr Claudia Wascher):

The authors have significantly revised the manuscript alongside with previous comments by the reviewers. The reviewers recommend the manuscript to be accepted for publication, they only ask the subtitle to be deleted.

Reviewer comments to Author:
Reviewer: 1
Comments to the Author(s)
The changes addressed my concerns- looks good.

Reviewer: 2
Comments to the Author(s)
The authors have taken the reviewers' comments to heart and greatly clarified their manuscript. The distinction between "cost" and "price" is especially helpful.

The only change I would recommend is the deletion of the subtitle. I does not seem necessary. The title alone summarizes the manuscript's main finding.

Author's Response to Decision Letter for (RSOS-191231.R0)

See Appendix B.

Decision letter (RSOS-191231.R1)

13-Aug-2019
Dear Ms Mihalik,

I am pleased to inform you that your manuscript entitled "Trophy hunters pay more to target larger-bodied carnivores" is now accepted for publication in Royal Society Open Science.

You can expect to receive a proof of your article in the near future. Please contact the editorial office (openscience_proofs@royalsociety.org and openscience@royalsociety.org) to let us know if you are likely to be away from e-mail contact -- if you are going to be away, please nominate a co-author (if available) to manage the proofing process, and ensure they are copied into your email to the journal.

Due to rapid publication and an extremely tight schedule, if comments are not received, your paper may experience a delay in publication.

Royal Society Open Science operates under a continuous publication model (http://bit.ly/cpFAQ). Your article will be published straight into the next open issue and this will be the final version of the paper. As such, it can be cited immediately by other researchers.
As the issue version of your paper will be the only version to be published I would advise you to check your proofs thoroughly as changes cannot be made once the paper is published.

On behalf of the Editors of Royal Society Open Science, we look forward to your continued contributions to the Journal.

Kind regards,

Lianne Parkhouse
Editorial Coordinator
Royal Society Open Science
openscience@royalsociety.org

on behalf of Dr Claudia Wascher (Associate Editor) and Kevin Padian (Subject Editor)
openscience@royalsociety.org

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Big game hunters pay more to target larger-bodied carnivores: insight from costly signalling money, guns, and costly signalling signals theory in non-subsistence systems

Ilona Mihalik¹,²*, Andrew W. Bateman¹,², and Chris T. Darimont¹,²

¹Department of Geography, University of Victoria, Victoria, British Columbia, Canada
²Raincoast Conservation Foundation, Sidney, British Columbia, Canada
*corresponding author: ilonammillie@gmail.com
Keywords: body size, costly signalling, trophy hunting, wildlife harvest, exploitation, carnivore, size-selective harvesting

1. Abstract

Hunters often target species that require resource investment disproportionate to associated nutritional rewards. Although a controversial theory, costly signalling provides a potential explanation, proposing that hunters may provide an explanation if human suggests that subsistence and non-subistence hunters evolved behaviour to target species that impose high ecological costs (e.g., higher failure and injury risks, lower consumptive returns) because it signals, thereby signaling to potential mates or competitors their ability to absorb such costly behaviour. If costly signalling is relevant to contemporary ‘big game’ hunters, and if prices for guided hunts reflect desirability, we would expect non-subistence hunters to pay higher prices to hunt taxa with higher associated perceived ecological costs. Accordingly, among guided hunters, we hypothesized that hunt prices would be higher for taxa with higher perceived ecological costs: those that are larger-bodied, rarer, carnivorous, or described as dangerous or difficult to hunt. In a data set on 721 guided hunts for fifteen North American big-game species, prices listed on the internet did not vary with rarity or perceived danger or difficulty but increased with body size in carnivores (from approximately $550 USD/day to $1800 USD/day across the observed range) in carnivores. This pattern suggests that elements of costly signals may persist among contemporary and non-contemporary non-subistence hunters. Persistence might simply relate to deception, given that despite unlikely signal honesty and any fitness benefits being unlikely in such radically different hunting systems, radically different social and ecological and technological conditions compared
with ancestral environments in which hunting behaviour evolved... More broadly, we did not find a signal of rarity or perceived danger or difficulty. Larger-bodied carnivores are generally more desirable to hunters due to perceived benefits of costly signalling, then conservation and management strategies should consider not only the ecology of the hunted but also the motivations of hunters.

2. Introduction

The behaviour of human hunters and fishers diverges substantially from other predators of vertebrate prey. Instead of targeting mainly juvenile or otherwise vulnerable individuals, humans (and more often, males), typically seek large taxa, as well as large, and reproductive-aged individuals within populations, a behaviour also found in phenotypes targeted by early human groups. This distinct pattern of hunting behaviour is likely shaped by a suite of adaptive selective forces; for example, in subsistence societies, provisioning targeting large prey items may be motivated by kin provisioning among kin family members is clearly important (has likely been favoured by kin selection; "provisioning model"); whereas, Likewise, on the other hand, sharing... Likewise...
sharing meat from large items to prey beyond kin, and expecting the same in return, may present an example of reciprocal altruism.\textsuperscript{12,13} Additional patterns of hunting behaviour have informed other evolutionary models.\textsuperscript{67}\textsuperscript{68} Explanations underlying explain hunting behaviour. Within traditional hunter-gatherer groups, for example, male hunters often target species with a highly variable caloric payoff over more reliably or safely acquired alternatives.\textsuperscript{14,15} Similarly, particularly in trophy-hunting contexts, contemporary hunters have pursued taxa that are rare and have historically exploited populations (especially terrestrial carnivores) at high rates compared to non-human predators.\textsuperscript{16,17} To seek their prey, modern hunters often are often motivated to travel to unfamiliar areas and pay large fees to travel to unfamiliar areas and hire specialist guides.\textsuperscript{18} Prices for guided hunts can be substantial, ranging from several hundred to many thousands of US dollars per day.\textsuperscript{2,4} In addition, permits to hunt some species can reach tens of thousands of USD.\textsuperscript{9} Additionally, owing to restrictions on meat exports, and to the targeting of seldom-eaten species, such as large carnivores, modern hunters have historically made the large investments required for guided hunts frequently see.\textsuperscript{18}\textsuperscript{20} People made without the intention of receiving nutrition, the primary benefit of predation in the wild. Such seemingly counterintuitive seemingly inefficient behaviour begs the question: how did such seemingly inefficient hunting behaviour evolve, and why might it persist today?
Ostensibly wasteful investments by animals have long intrigued researchers, inspiring theory, empirical investigation, and debate. Darwin, for example, questioned what drove the evolution of extravagant traits in males, such as the large tails of peacocks (Pavo spp.) and antlers of deer (Cervidae). Zahavi proposed that time-consuming, risky, inefficient, or otherwise ‘handicapping’ traits or activities could be interpreted as ‘costly signals.’ Costly signalling theory suggests that a costly signal (or ‘handicap’) reflects the capacity of the signaler to bear the cost, therefore providing honest information to potential mates and competitors about the underlying quality of the signaler (e.g., the ‘strategic cost’). The theory suggests that honesty is maintained through the differential costs and benefits of signal production; individuals of higher quality are thought to be better able to afford the larger costs associated with more elaborate attractive signals; for lower-quality individuals, while the costs outweigh the benefits and signals are difficult to fake for lower-quality individuals. Under this framework, evolutionary benefits flow to higher-quality signalers (as well as the signal recipients), the signaler. Individuals that can afford costly signals attract mates and accrue social status, which can increase access to resources (e.g., foods, material goods, approval from peers, knowledge). For example, in avian courtship displays male birds subject themselves to predation risk by singing or dancing in the open during sexual displays, signalling that they have underlying qualities that permit them to absorb the energetic and predation-risk costs of the display. Similarly, in human systems, costly signalling has been used to explain behaviour associated with artistic elaboration, ceremonial feasting, body modification, and monumental architecture. Individuals that can afford costly signals can attract mates or accrue social status, which can increase access to...
resources (e.g., foods, material goods, approval from peers, knowledge). Using similar logic, sociologists use the term ‘conspicuous consumption’ to describe the purchase and display of luxury goods and activities. Although costly signalling and associated theory is not universally accepted, it provides a useful framework with which to evaluate apparently inefficient behaviour. Whereas data are limited and debate common, costly signalling has also been invoked to explain hunting behaviour in some human subsistence-hunting systems, although relevant data are limited and debate is common. According to the theory in this context, when subsistence hunters target, hunting behaviour by humans is multifaceted and not mutually exclusive, often motivated by provisioning oneself, kin, and/or through reciprocal altruism, while certain behaviour hunting by humans has also can also been considered in a costly signalling framework. Even in the case of subsistence hunting within traditional hunter-gather groups, male hunters often target species with a highly-variable caloric payoff over more reliably or safely acquired alternatives. In targeting items with high ecologic costs, they (i.e., risk of failure, injury, etc), such hunters would honestly signal their ability to absorb the costs. Thus, according to this theory, hunting itself serves as the signal, and successfully or hunting a species with higher costs signals produces a higher quality signal (akin to a more showy avian courtship display). Hunting of marine turtles (Chelonia mydas) by the Meriam peoples of Murray Island, Northern Australia, provides an example. There, diverse members of Meriam society collect marine turtles as they crawl on the beach where they are easily captured; however, only reproductive-aged men...
participate in off-shore turtle hunting, a costly activity (i.e., high risk of failure; increased risk of injury; lower consumptive returns; high energetic, monetary, time investment costs). When successful, these hunters rarely consume the meat themselves, and instead provision community members at large feasts, arguably providing the public forum to signal the hunters’ underlying qualities that allow them to engage in such costly behaviour. Successful Meriam turtle hunters earn social status and higher reproductive success, providing rare evidence for fitness benefits associated with apparent costly signalling in humans. Men from other hunter-gatherer societies suggested to exhibit similar signalling behaviour, not easily explained by provisioning or reciprocal altruism alone, include the Ache men of Eastern Paraguay, the Hadza men of Tanzania, and male torch fishers of Ifaluk. However, some criticisms of these interpretations include whether men’s hunting patterns are truly suboptimal in terms of nutrient acquisition (e.g., argued in the case of the Hadza men), and that Hadza and Ache men value provisioning over showing-off their hunting ability, regardless of having dependent offspring. Additionally, others argue that fitness benefits gained by hunters are influenced by multiple pathways, rather than just through showing off.

Although a controversial theory when applied to examining costly signalling may help to human explain elements of non-subsistence hunting, examining seemingly wasteful hunting behaviour among non-subsistence hunters (hunting without the goal of providing food, e.g. trophy hunting) offers new opportunity to confront elements of this controversial theory. Costly signalling may help to explain or not seemingly wasteful inefficient non-subsistence
hunting behaviour that among non-subsistence hunters appear to conforms to predictions of costly signalling theory might provide fresh new insight into the discussion about hunting. In particular, as explained above, non-subsistence trophy hunters would supposedly seemingly appear to incur substantial costs in terms of high failure risk or risk of injury as well as low to nil consumptive returns when they target large-bodied, carnivorous, rare, and/or dangerous or difficult-to-hunt species. Specifically, we would expect increased failure risk via lower hunter-encounter rates with larger and higher trophic-level animals, which tend to occur at lower densities than small, low-trophic-level species. Similarly, hunters likely encounter other rare species of high conservation concern (with populations reduced by human impacts) less frequently than abundant species of low conservation concern. In addition, species that are dangerous or difficult to hunt are likely to increase failure and injury risk, posing another cost, owing to injury or unsuccessful attempts. Moreover, human hunters often kill seldom-eaten species, such as carnivores, which includes the opportunity cost of forgoing greater nutrition from hunting edible prey. Collectively, hunting inefficiently by targeting such inefficient prey characteristics could signal a perceived perceived ability to accept the costs of higher failure and injury risk, as well as opportunity costs, compared with targeting species that are more easily secured and offering higher nutritional return. Throughout this paper, we use the term "cost" to refer to these cost of forgoing greater nutrition from hunting edible prey. Collectively, hunting inefficiently by targeting such inefficient prey characteristics could signal a perceived perceived ability to accept the costs of higher failure and injury risk, as well as opportunity costs, compared with targeting species that are more easily secured and offering higher nutritional return. Throughout this paper, we use the term "cost" to refer to these cost of forgoing greater nutrition from hunting edible prey. Collectively, hunting inefficiently by targeting such inefficient prey characteristics could signal a perceived perceived ability to accept the costs of higher failure and injury risk, as well as opportunity costs, compared with targeting species that are more easily secured and offering higher nutritional return. Throughout this paper, we use the term "cost" to refer to these cost of forgoing greater nutrition from hunting edible prey. Collectively, hunting inefficiently by targeting such inefficient prey characteristics could signal a perceived perceived ability to accept the costs of higher failure and injury risk, as well as opportunity costs, compared with targeting species that are more easily secured and offering higher nutritional return. Throughout this paper, we use the term "cost" to refer to these cost of forgoing greater nutrition from hunting edible prey. Collectively, hunting inefficiently by targeting such inefficient prey characteristics could signal a perceived perceived ability to accept the costs of higher failure and injury risk, as well as opportunity costs, compared with targeting species that are more easily secured and offering higher nutritional return. Throughout this paper, we use the term "cost" to refer to these.
we argue the behaviour still persists due to benefits provided by costly signaling in previous conditions (i.e. mismatch theory). Indeed, showing off risky game was perhaps once advantageous throughout ancestral hunter-gatherer periods of human evolution (and still adaptive in some modern-day hunter-gatherer groups). However, fitness benefits from hunting big game today are difficult to measure within the developed world, even if the tendencies are still ingrained. Although, elaborate a similar to the avian courtship displays and offshore turtles hunting in Meriam society, hunting behaviour that targets such costly prey might signal otherwise hidden qualities, physical competency, or cognitive ability. Awards from, and status hierarchies within, organizations with large followings like Safari Club International (SCI) provide evidence of modern-day status benefits to signalers; SCI offers dozens of elaborate awards that create status hierarchies among members; for guided hunts, example, to achieve the World Hunting Award one must have already achieved 11 Grand Slam Awards, 17 diamond-level Inner Circle Awards, and both the Fourth Pinnacle of Achievement and Crowning Achievement Award.

Although the targeting of some big-game (i.e., relatively-large species mammals hunted for sport) by modern contemporary non-subsistence hunters appears to include many elements of costly signalling behaviour, there have been no empirical evaluations of the theory in this context. If such trophy hunting behaviour is an example of reflects elements of costly signalling that persists among contemporary human hunters, we would predict that species with high perceived costs should be more desirable to hunters because they could signal a greater ability to absorb the costs. Accordingly, assuming that market demand (which could also be influenced by lower supply in the case of rare species)
causes influences price to reflect desirability -- (a common assumption 15, 21, 22) -- we hypothesized that hunt prices would be higher, and accordingly hunters would be willing to pay, for taxa with higher perceived ecological costs of hunting. We note that lower supply, through rarity or hunting restrictions, could also drive up prices, but we would not expect to find an association with prey body size, or hunt danger, or difficulty in this case. We confronted this in our hypothesis using data from guided big-game trophy hunting systems, where most hunters hire specialist guides.36 Prices for guided hunts can be substantial, ranging from several hundred to many thousands of US dollars (USD) per day. In addition, permits to hunt some species can reach tens of thousands of USD.38 Specifically, using price charged per day for guided hunts as an index, we predicted that species that are 1) large-bodied, 2) rare, 3) carnivorous, and 4) described by Safari Club International (SCI)37 as dangerous or difficult-to-hunt, would be priced higher. In other words, we predicted that guided hunters would pay higher prices for hunts that signal ecologically costlier behavior.

3. Data Collection and Methods

Species included

We collected prices advertised for guided hunts of 15 North American big game species (Table 1). We selected these species because they comprise the species requirements of SCI’s Grand Slam North American 29 award, which requires hunters kill 29 of the 38 North American species or subspecies.38

Price data
We collected data on prices advertised online by hunting guides for each species in every North American province and state in which species occurred (n = 160 species-jurisdiction combinations). Data collection occurred between November 2017 and January 2018. We used consistent web searches using Google search engine, changing only the jurisdiction or species name for each new search. The goal was to obtain the first five unique prices from each search. Forty-six of the 160 search combinations, however, revealed fewer than five results (mean = 2.37, range: 1 to 4). Owing to particularly low sample size for polar bears (originally, two), we collected four additional polar bear prices in June 2018. For these we used the term, “arctic” in place of the jurisdiction and altered the order of wording. From all price data, we calculated an average price/day.

Websites presented a variety of options to hunters, requiring a standardization approach. We excluded websites that either did not include prices or stated to “call or email for prices”. We focused on free-range (i.e. not fenced) hunts targeting males during the rut (for ungulates) if different seasons were available. Prices included guiding, meals, and accommodation. We did not include baited hunts or ‘combination’ hunts that included more than one species for one price. We chose rifle hunts when hunters were given options (usually among rifle, muzzleloader, archery), and muzzleloader was chosen if rifle was not an option. If neither were available (n = 3), archery hunt prices were converted to firearm prices by using the average ratio (rifle price/archery price; 1.20) calculated from those with a choice (n = 26).

We estimated the contribution of charter flights to total cost to remove that component from prices that included it (n = 49). We subtracted the average flight cost if included, calculated from
hunts that stated the cost of a charter for the same species-jurisdiction. If no estimates were available, the average flight cost was estimated from other species within the same jurisdiction, or from the closest neighbouring jurisdiction. Similarly, trophy and license/tag fees (set by governments in each province and state) were removed from prices if they were advertised to be included.

We also estimated a price-per-day from hunts that did not advertise the length of hunt. We used data from websites that offered a choice in the length (i.e. three days for $1000, five days for $2000, seven days for $5000), and selected the most common hunt-length from other hunts within the same jurisdiction. We used an imputed mean for prices that did not state the number of days, calculated from the mean hunt-length for that species and jurisdiction.

Overall we obtained 721 prices for 43 jurisdictions from 471 guide businesses. Most prices were listed in US Dollars, including those in Canada. Ten Canadian results did not state the currency and were assumed as USD. We converted CAD results to USD using the conversion rate for November 15, 2017 (0.78318 USD per CAD).

**Body mass**

Mean male body masses for each species were collected using three sources. When mass data were only available at the subspecies-level (e.g. elk, bighorn sheep), we used the median value across subspecies to calculate species-level masses.

**Rarity**
We used the provincial or state-level conservation status (the subnational rank or “S-Rank”) for each species as a measure of rarity. These were collected from the NatureServe Explorer. Conservation statuses range from S1 (Critically Imperilled) to S5 (Stable) and are based on species abundance, distribution, population trends, and threats. Some ranks denote uncertainty within a range and fall in-between two ranks (e.g., S1S2; S2S3 etc.). Accordingly, we converted ranks to 1, 1.5, 2, 2.5, 3, 3.5, 4, 4.5, 5.

**Classification: ungulate vs carnivore**

We categorized species as either “carnivore” or “ungulate”. Carnivore includes species of the order Carnivora and ungulate includes species with hooves (Table 1).

**Difficult or dangerous**

Whereas larger, rarer and carnivorous animals would carry higher costs owing to lower densities, we additionally considered other species characteristics that would increase cost due to risk of failure or potential injury. Accordingly, we categorized hunts for their perceived difficulty or danger. We scored this variable by inspecting the ‘remarks’ sections within SCI’s online record book, similar to the qualitative exploration of SCI remarks by Johnson et al., (2010). Specifically, species hunts described as ‘difficult’; ‘tough’; ‘dangerous’; ‘demanding’, etc. were noted. Species with no hunt descriptions or described as being ‘easy’; ‘not difficult’; ‘not dangerous’, etc. were scored as not risky. SCI record book entries are often described at a subspecies-level with some subspecies described as difficult or dangerous and others not, particularly for elk and mule deer subspecies. Using the subspecies range maps in the SCI record
book, we categorized species hunts as presence or absence of perceived difficulty or danger only in the jurisdictions present within the subspecies range.

Statistical methods

We employed information-theoretic model selection using Akaike’s information criterion (AIC) to gauge support for different hypotheses relating our selected predictors to hunting prices. In general terms, AIC rewards model fit and penalises model complexity, to provide an estimate of model performance and parsimony. Before fitting any models, we constructed an a priori set of candidate models, each representing a plausible combination of our original hypotheses (see Introduction).

Our candidate set included models with various combinations of our potential predictor variables as main effects. We did not include all possible combinations of main effects and their interactions, and instead evaluated only those that expressed our hypotheses. We did not include models with (ungulate vs carnivore) classification as a term on its own. Given that some carnivore species are commonly perceived as pests (e.g. wolves) and some ungulate species are highly prized (e.g. mountain sheep), we did not expect a stand-alone effect of classification. We did consider the possibility that mass could influence the response differently for different classifications, allowing for an interaction between classification and mass. Following similar logic, we considered an interaction between SCI descriptions and mass. We did not include models containing interactions with conservation status as we predicted rare species to be expensive regardless of other characteristics. Similarly, we did not include models containing interactions between SCI descriptions and classification; we assumed that species described as
difficult or dangerous would be more expensive regardless of their classification as carnivore or ungulate.

We fit generalized linear mixed effects models, assuming a gamma distribution with a log link function. All models included jurisdiction and species as crossed random effects on the intercept. We standardized each continuous predictor (mass and conservation status) by subtracting its mean and dividing by its standard deviation. We fit models with the lme4 package version 1.1-

21 in the statistical software R 45. For models that encountered fitting problems using default settings in lme4, we specified use of the nlminb optimization method within the optimx optimizer46, or the bobyqa optimizer47 with 100000 set as the maximum number of function evaluations.

4. Results

We compared models including combinations of our four predictor variables to determine if prey with higher perceived costs were more desirable to hunt, using price as an indication of desirability. Our results suggest that hunters pay higher prices to hunt species with certain 'costly' characteristics, but do not provide support for all our hypotheses. Our highest ranking model (Table 2) included mass, classification, and their interaction (Figure 1). The interaction term between mass and classification (coefficient estimate = 0.38, 95% CI 0.08 to 0.69) indicated that hunt price increased with body mass in carnivore species but was not influenced by changing ungulate body mass. Model predictions show that prices charged to hunt carnivore species increased from approximately $550 USD/day to $1800 USD/day across the variation in
body mass, while prices remained at approximately $900 USD/day for ungulate species regardless of their body size (Figure 1).

Although the highest ranking model did not have overwhelming support (Akaike model weight, \( AIC_w = 0.23 \)), the trend of higher prices for larger carnivores was consistent throughout our results, including two other models within the top-model set (\( \Delta AIC < 2 \)). Due to recent debate in the literature regarding methods to determine the importance of multiple processes, we also present results in the supplementary material from the model-averaged and global models. Results were qualitatively unchanged (Figure S1a,b).

SCI descriptions and rarity were not included within the top model and did not have a meaningful influence on price. SCI was included in the third-ranking model (\( \Delta AIC = 1.543, AIC_w = 0.11 \)); however, the confidence interval for the effect overlapped zero (coefficient estimate = 0.06, 95% CI -0.12 to 0.24). Rarity, based on species’ jurisdiction-level conservation statuses was included in the fourth-ranked model (\( \Delta AIC = 1.6458, AIC_w = 0.104 \)), and its confidence interval also overlapped zero (coefficient estimate = 0.01, 95% CI -0.03 to 0.05).

Although both predictors did appear in the top model set, their effects were minimal in the model-averaged and global model results (Figure S2a, b; Figure S3a,b).

5. Discussion

At a North American continental scale, we analysed guided trophy hunting in the context of costly signalling theory. We examined hunting as a signal, and the risks of failure and injury, as well as opportunity costs related to low consumptive returns, as the potential associated
ecological costs. We asked if characteristics of prey associated with higher perceived costs were correlated with higher prices charged to hunters (which we assume to represent a market-mediated index of desirability). We argue that costly signalling theory might provide an evolutionary explanation for why big-game hunters target specific species. We found some support for our prediction, showing that hunters pay more to kill larger-bodied carnivores, which likely carry higher perceived risk of failure and injury, as well as low consumptive returns, and are therefore perceived as more costly, as we argue below.

Some patterns we observed differed from previously published findings. For one, the jurisdiction-level conservation status (state or provincial-level within North America) of a species (our proxy for rarity) did not affect price in our analysis. In contrast, larger-scale conservation rankings (such as IUCN and/or CITES) have previously been found to correlate with hunting price in Caprinae species, Bovidae taxa, ungulates, and African felids. Two explanations for why we did not detect a relationship might be relevant. First, the jurisdiction-level rankings showed little variation across species in our data set; only 18% (n = 27) of the species-jurisdiction combinations ranged from ‘Vulnerable’/’ Apparently Secure’ (S3/S4) to ‘Critically Imperiled’ (S1). The remainder were not classified as at risk. Second, hunters (especially when they commonly originate from afar) might not know or consider the jurisdiction-level conservation status (which were included in our models) of their targets, whereas a species’ IUCN ranking is typically well-known and often included in their SCI record book descriptions. However, only two species used in our study were ranked by the IUCN as “Vulnerable”, while the remaining thirteen ranked as “Least Concern”.
We found that the presence of a ‘difficult and/or dangerous’ hunt description by SCI likewise had no statistical influence on price. This result departed from our predictions, given that difficult and dangerous descriptions should increase the perception of failure risk and risk of injury. We speculate that, unlike subsistence hunts (which likely carry realistic and meaningful risk of failure), guided big game hunters in reality risk relatively little in terms of failure owing to difficulty or danger. Contemporary hunters now employ efficient killing technology to hunt prey at a safe distance. Indeed, while we expected the perception of difficulty and danger to matter in terms of desirability, guided hunts that pose real risks to safety might be relatively uncommon, and customers guided clients (and those to whom hunting signals are broadcast) are likely to be aware of this.

Our work has several potential limitations. Among them, we assume that prices charged to hunt different species reflect desirability for hunters, an assumption commonly made in the literature on the Anthropogenic Allee Effect (AAE). Similarly, we assumed rarity to be more desirable owing to lower supply. Additional factors are likely also involved. While we did not address it in our study, due to the coarse state- or province-scale resolution of available data, the cost of living (food, accommodation, and guiding) may also influence prices. Given that the two largest carnivores (polar and grizzly bears) in our data-set occur at northern latitudes, associated with remoteness and high costs of living, this was of concern. Accordingly, we post hoc examined whether latitude could explain the high hunt prices observed for large carnivores. While large carnivores do tend to occur at higher latitudes (Figure S4), we found no statistical evidence that latitude drove hunt price for carnivores (Figure S5). Additionally, some might argue that pursuing larger-bodied carnivores might have additional costs related to
searching for targets, given their naturally low density. This is possible, but we standardized our
daily rates, dealing with the possibility that lower density species might take
ger longer to locate. Furthermore, the use of an imputed mean for hunts without a listed duration,
calculated by using the mean hunt-length for a species-jurisdiction (combination of each species
in every North American province and state in which they occur), could lead to biased results
for carnivores (if they do indeed require additional search times). Finally, we acknowledge
Google’s search results may vary across users and limit reproducibility.

We speculate that the relationship between body mass and price is evident only in
carnivores (Figure 1) because larger size in these taxa strongly signal increased
perceived measures of danger, or, rarity and other costs not accounted for in our analysis.
Specifically, although not captured in SCI descriptions, larger-bodied carnivores could give the
perception of increased danger; displaying a carcass of a predator could signal the absorbed costs
of interacting with animals that, compared to ungulates, are perceived as more dangerous if they
are larger-bodied. Additionally, larger-bodied carnivores are naturally rarer, owing to their
higher trophic position. This dimension of rarity (perceived rarity) could be recognized
by hunters and could therefore serve as a better proxy for rarity compared with conservation
status, especially on a continent where few hunted taxa are of dire conservation concern. Finally,
unlike herbivores, carnivores are generally not consumed, imposing the additional cost of
receiving no nutritional gains from kills. Only the smaller bodied black bear (classified here
as a carnivore) is commonly eaten. Whereas these explanations are speculative, they generally
align with previous research that has found North American hunters display evidence of
‘achievement satisfaction’ (congruence of goals and outcomes regarding performance) more
commonly when sharing information about carnivore hunts compared to herbivore hunts. For example, men posing with ungulates bearing larger antlers ornaments, and carnivores of any size; in hunting photographs have greater odds of displaying a ‘true smile’, an honest signal of pleasure compared to pictures with herbivore prey. Additionally, in online discussion forums about hunting, men express achievement-oriented phrases more frequently when describing carnivore hunts compared to ungulate hunts.

Our results, showing increased value placed by hunters on large-bodied prey, share similarities with work conducted in other areas that adopted a different line of conceptual inquiry. Specifically, the anthropogenic Allee effect (Effect (AAE)) describes a phenomenon in which rare species become more desirable to hunters. In this context, others have similarly found that body size positively correlates with hunting prices, specifically in ungulates and African species. Our results thus increase the scope of taxa and contexts involved in the pattern, suggesting that, although not universal, the desire of hunters to kill larger species exists across different environments, cultures, conservation contexts, and communities of species available for hunting. This observation of similar patterns across diverse systems of contemporary hunting suggests the potential for an underlying evolutionary origin of the behaviours involved.

Might costly signalling explain the evolution and maintenance of otherwise inefficient behaviour and displays? The theory is not universally accepted, argued by some to be particularly misapplied in studies of
One important consideration is that apparently costly signalling systems are potentially subject to cheating by modern humans. One possibility in our systems is that guided hunters in fact pay money to buy experiences that in effect deceive recipients of costly hunting signals; despite a near absence of real risk of failure and injury, they pay more to signal greater perceived costs. We suspect that signals broadcast by contemporary hunters are likely no longer honestly linked to cognitive/physical qualities (due to expert guides and efficient weaponry). We did not evaluate any fitness benefits of costly considered in our study as a 'cost', prices paid to hunt a species represent significant costs in today’s monetary-based currency. Thus, guided hunters might additionally signal their financial ability to afford such expensive pursuits. A fitness benefits of costly signalling among guided hunters, for example, has not been evaluated but also such benefits seem unlikely. Persistence of evolutionarily-mismatched behaviours, however, is common in contemporary human society (e.g. gambling and risk-taking in adolescents) and perhaps seems likely in our case, given such rapid and extraordinary change in likely differences between current social
and ecological conditions compared to the ancestral environments in which hunting behaviour evolved. Though we suspect that signals shown-off by contemporary hunters are likely no longer be honestly linked to cognitive/physical qualities (due to expert guides and efficient weaponry purchased by hunters), and perhaps not adaptive, we argue the behaviour still persists due to benefits of evolutionarily mismatched behaviours, which hunting behaviour evolved. However, due to benefits provided by costly signaling in previous conditions (i.e. mismatch theory). Indeed, showing off risky game was perhaps once advantageous throughout ancestral hunter-gatherer periods of human evolution (and still adaptive in some modern-day hunter-gatherer groups), however, fitness benefits from hunting big game today are difficult to measure within the developed world, even if the tendencies are still ingrained. Although, any fitness benefits of costly signaling among guided hunters also seem unlikely. Instead, elaborate awards from, and status hierarchies within, organizations with large followings (e.g. like Safari Club International (SCI)) provide evidence of modern-day status-social benefits to signallers. Although there is general societal disapproval for trophy hunting, SCI offers dozens of elaborate awards that create status hierarchies among members; for example, to achieve the World Hunting Award one must have already achieved 11 Grand Slam Awards, 17 diamond-level Inner Circle Awards, and both the Fourth Pinnacle of Achievement and Crowning Achievement Award. Beyond these SCI award recipients, however, normative general societal disapproval might in fact function to shame trophy hunters. Future studies could assess the relationships between costs absorbed and measures of related social status earned. With an online and increasingly globalized audience, examinations of
the support (e.g., ‘likes’ or other positive feedback received on social media platforms) in
different big game hunting contexts could yield new insight. Work is also required to examine
the potential benefits flowing to audience members (the signal recipients), asking what
information on signaller quality might be assessed.

Additional possibilities need to be considered in evaluating hunting behaviour in
trophy hunting systems. Specifically, costly signaling theory is argued by some to be particularly misapplied in studies of contemporary human
behavior. One important consideration is that generally, apparently costly signals are
potentially subject to cheating by modern humans. In our system, with only minimal
real risk of failure or injury, guided hunters might simply pay money to buy experiences that in
effect serve to deceive signal recipients of costly hunting signals; despite a near absence of real
risk of failure and injury, hunters pay to signal costs. We suspect that signals broadcast by
contemporary hunters are likely no longer honestly linked to cognitive or physical qualities (due
to expert guides and efficient weaponry). Accordingly, all that is required for such
deception to occur is for hunters to desire costly prey. Whereas in the past, underlying qualities
were necessary to hunt costly prey, today’s guided hunters can simply buy such opportunities via
a mechanism (money) and context with no fitness-related penalties of cheating. If
true, this behaviour is similar to the purchase and display of luxury or brand-named goods and
activities, termed ‘conspicuous consumption’ by sociologists.
Regardless of underlying behavioural context, hunters showing increased desire to kill large carnivores might provide additional insight into why large carnivores have been exploited at such high rates in the past\textsuperscript{40-61,63} and present\textsuperscript{36} continue to be exploited at such high rates.\textsuperscript{36}

Although there is disagreement among on the impact of trophy hunting on population dynamics of prey\textsuperscript{64-66}. The patterns revealed in our work and that of others\textsuperscript{15-19,64} suggest that management strategies for vulnerable wildlife should also consider how not only population dynamics of prey but also how different hunting policy might alter the potential costs, signals, and social benefits to hunters.

Using similar logic, sociologists use the term ‘conspicuous consumption’ to describe the purchase and display of luxury goods and activities\textsuperscript{36}.
Data Accessibility

All raw data and R code for analysis are included in the Dryad Depository:
https://datadryad.org/review?doi=doi:10.5061/dryad.b1k2979

Research Ethics – *Heading does not apply to our manuscript*

Research Ethics was not applicable. We were not required to complete an ethical assessment prior to conducting the research.

Animal Ethics – *Heading does not apply to our manuscript*

Animal Ethics was not applicable. We were not required to complete an ethical assessment prior to conducting the research.

Permission to Carry out Fieldwork – *Heading does not apply to our manuscript*

No permissions to carry out fieldwork were required prior to conducting the research.

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Competing Interests

The authors declare no competing interests.

Author Contributions

IM and CTD conceived and designed the study. IM collected the data. IM and AWB analyzed the data and prepared figures. IM, CTD, and AWB wrote the manuscript.

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Figure 1. Effect of mass on daily guided-hunt price for carnivore (orange) and ungulate (blue) species in North America. Points show raw mass for carnivores and ungulates, curves show predicted means from the maximum-parsimony model (see text), and shading indicates 95% confidence intervals for model-predicted means.
Table 1. North American “big game” species included in our study.

| Species (common)     | Latin                  | Classification |
|----------------------|------------------------|----------------|
| Mountain Lion        | *Puma concolor*        | Carnivore      |
| Black Bear           | *Ursus americanus*     | Carnivore      |
| Brown Bear           | *Ursus arctos*         | Carnivore      |
| Polar Bear           | *Ursus maritimus*      | Carnivore      |
| Muskox               | *Ovis moschatus*       | Ungulate       |
| Gray Wolf            | *Canis lupus*          | Carnivore      |
| Thinhorn Sheep       | *Ovis dalli*           | Ungulate       |
| Bighorn Sheep        | *Ovis canadensis*      | Ungulate       |
| Caribou              | *Rangifer tarandus*    | Ungulate       |
| Pronghorn            | *Antilocapra americana* | Ungulate     |
| White-tailed Deer    | *Odocoileus virginianus* | Ungulate    |
| Moose                | *Alces alces*          | Ungulate       |
| Mule Deer            | *Odocoileus hemionus*  | Ungulate       |
| Mountain Goat        | *Oreamnos americanus*  | Ungulate       |
| Elk                  | *Cervus canadensis*    | Ungulate       |
Table 2. AIC evaluation of models for predicting prices of hunts offered by hunting guides. The explanatory variables were the average male body mass (Mass; in kg), the classification (Class; either carnivore or ungulate), descriptions of difficulty or danger in Safari Club International hunt descriptions (SCI; either absence or presence), and conservation status in jurisdiction (Status; 1, 1.5, 2, ..., 5).

| Model                                      | df | logLik     | ΔAIC | AICw |
|--------------------------------------------|----|------------|------|------|
| Mass + Class + Mass×Class                 | 7  | -487.7884  | 0.00 | 0.23 |
| Mass                                       | 5  | -488.0259  | 1.13 | 0.13 |
| Class + Mass + SCI+ Mass×Class             | 8  | -487.7845  | 1.54 | 0.11 |
| Class + Mass + Status + Mass×Class         | 8  | -487.7852  | 1.64 | 0.10 |
| SCI + Mass + SCI×Mass                     | 7  | -487.9874  | 2.06 | 0.08 |
| Status + Mass                              | 6  | -488.0978  | 2.17 | 0.06 |
| Class + Mass + SCI + Mass×Class + SCI×Mass | 9  | -487.7148  | 2.92 | 0.05 |
| SCI + Mass                                 | 6  | -488.1688  | 2.95 | 0.05 |
| Null (intercept only)                      | 4  | -488.2392  | 3.27 | 0.05 |
| SCI + Mass + Status + SCI×Mass             | 8  | -487.9598  | 3.82 | 0.04 |
| Status + Class + SCI + Mass + SCI×Mass + Mass×Class | 10 | -487.0240  | 4.65 | 0.02 |
| SCI + Mass + Status                        | 7  | -488.0171  | 4.67 | 0.02 |
| Status                                     | 5  | -488.2414  | 4.92 | 0.02 |
| SCI                                        | 5  | -488.2999  | 5.23 | 0.02 |
| SCI + Status                               | 6  | -488.1380  | 6.90 | 0.01 |
August 12, 2019

Dear Royal Society Open Science team,

Thank you for the opportunity to submit our revised manuscript “Trophy hunters pay more to target larger-bodied carnivores” RSOS-191231.R1, following your request for minor revisions.

We have addressed Reviewer 2’s comments and modified our manuscript’s title accordingly. We identify these changes below by using ** before our response. New or revised text are in italics.

We also upload a Track Changes version of the manuscript indicating these changes.

Sincerely,

Ilona Mihalik,
on behalf of Andrew Bateman and Chris Darimont

Associate Editor Comments to Author (Dr Claudia Wascher):

The authors have significantly revised the manuscript alongside with previous comments by the reviewers. The reviewers recommend the manuscript to be accepted for publication, they only ask the subtitle to be deleted.

** Thank you. We have made these changes.

Reviewer comments to Author:

Reviewer: 1

Comments to the Author(s)
The changes addressed my concerns- looks good.

** Thank you.

Reviewer: 2

Comments to the Author(s)
The authors have taken the reviewers' comments to heart and greatly clarified their manuscript. The distinction between "cost" and "price" is especially helpful.

The only change I would recommend is the deletion of the subtitle. It does not seem necessary. The title alone summarizes the manuscript's main finding.

** Thank you for your suggestion. We have removed the subtitle and our title now reads,

*Trophy hunters pay more to target larger-bodied carnivores*