

Comment



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Flawed analysis and unconvincing interpretation: a comment on Chapron and Treves 2016

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Chapron & Treves [1] (hereafter C&T) believe that quantifying poaching is ‘one of the most crucial questions for the conservation of large carnivores’ (p. 2). We agree that evaluating poaching is important and merits rigorous attention. Yet, we argue that C&T’s claim, ‘allowing culling increases poaching’, is not supported by their data. We assert that C&T is based on flawed analysis and unconvincing interpretation of scientific literature.

C&T claimed to ‘present the first quantitative evaluation of the hypothesis that culling will reduce poaching’. However, Olson *et al.* [2] used empirical data (fates of wolves) to demonstrate that illegal killing decreases with increasing availability of lethal depredation management (hereafter, LDM). C&T claimed to ‘show that allowing wolf [*Canis lupus*] culling was substantially more likely to increase poaching than to reduce it’. However, C&T produced no empirical evidence of increased poaching, but only showed a marginal association between policy change allowing LDM and reduction in expected wolf population growth in Wisconsin and Michigan (USA). Additionally, C&T later reported a misalignment in their dataset between wolf population size, number of wolves culled and policy change [3]. C&T claim that the conclusion of their ‘paper is still supported by the correct results’ (p. 1) [3]. However, the lack of a significant change in results following the correction of their data suggests either important design flaws or a phenomena largely uncoupled from their putative ‘policy signals’.

C&T also claimed ‘replicated quasi-experimental’ (p. 2) design because changes in policy led to variation in LDM authority [1]. C&T compared ‘treatment’ periods (periods with LDM) with ‘control’ periods (when wolves were federally protected). C&T’s replication claim implies independence among treatments with respect to effect of policy signals [1, p. 3], something most-certainly untrue. Authorization for LDM varied temporally [1] and spanned wolf-years [1] such that wolf-years 2003–2010 and 2012 associated with LDM authority, and 2011 and 1979–2002 did not [1, fig. 1]. Since Wisconsin and Michigan wolves increased continually during the 18 years of their analysis [4–6], the critical ‘policy signal’ was almost perfectly confounded by population size. Thus, claims of meaningful replication are dubious. C&T’s analysis is a worst-case design for disentangling effects of policy and population size.

C&T selectively chose to analyse a subset of wolf population and life-history data (1995–2012), yet these datasets extend to 1980 and 1989 for Wisconsin and

Michigan, respectively [5,6]. Inclusion of the full range of wolf population and life-history data would probably have produced contrary results because poaching rates were higher prior to 1985 in Wisconsin when wolves were federally protected [7]. Moreover, choosing an exponential model virtually assured that observed growth would differ from predicted growth at higher population densities because exponential growth is unsustainable due to negative density-dependence—an axiom in population biology [8]. C&T justified an exponential model by claiming that density-dependence ‘would be a weakly identifiable parameter with poaching’ (p. 5). This is an implicit admission that C&T lacked the capacity to differentiate between effects of poaching and density-dependence in their model. This suggests that C&T either misunderstood the functional link between their model structure and the biological processes emulated or they ignored this limitation.

The above concerns notwithstanding, C&T admitted that ‘negative density dependence was the most intuitive explanation for reduced growth’ (p. 5). They claimed that ‘as with prior studies on Wisconsin’s wolf population’, they ‘did not detect any negative density dependence’ (p. 5). This statement is incorrect. Despite use of the plural (studies), C&T cite only Stenglein *et al.* [9] as support. However, Stenglein *et al.* [9, fig. 3] did provide evidence of negative density-dependence. C&T also ignored numerous publications demonstrating evidence of negative density-dependence in Wisconsin [4] and elsewhere (electronic supplementary material).

C&T claimed that ‘poaching was the most parsimonious explanation for observed decreases in wolf population growth rates, because [they] could rule out alternative plausible biological explanations’ (p. 5). Neither assertion is true. C&T evaluated only three life-history mechanisms for density dependence: wolf pack reproduction, wolf pack size, and area occupied by wolf packs. These three life-history features are not a comprehensive set of life-history mechanisms that could contribute to negative density-dependent growth in wolves given the scientific literature (electronic supplementary material). Additionally, while the most parsimonious hypothesis is not valid purely on the basis of simplicity, parsimonious hypotheses benefit from shorter chains of inference. Longer chains of inference require more evidence.

At least three non-exclusive hypotheses might explain the recent growth discrepancy observed by C&T: C&T’s devaluation hypothesis [1], the frustration hypothesis [2] or negative density dependence (electronic supplementary material). Of these, the chain of inference for the devaluing hypothesis is longest and indistinguishable from the frustration hypothesis, while density dependence is the most parsimonious and well-supported (electronic supplementary material). C&T dismiss the frustration hypothesis [2], arguing that frustration with wolf management was present prior to LDM authority (p. 5). But there is no evidence that devaluation of wolves was exclusive to the period after implementation of LDM. Similarly, poaching has always been a feature of the population biology of Great Lakes wolves and occurred at higher rates prior to 1985 when wolves were fully protected and there was no ‘policy signal’ [7]. Frustration with wolf management probably correlates with devaluing of wolves despite C&T’s assertion that devaluing depends on a specific and discrete outcome of changing policy.

C&T claimed that changes in policy associated with LDM prompted immediate devaluing of wolves, leading to

increased poaching sufficient to reduce population growth. Embedded in their claim of a ‘quasi-experimental design’ [1] is an assumed cycle of public valuing and devaluing that occurred repeatedly as authority for LDM varied over time. Effectively, C&T claimed that when states had LDM authority, the public devalued wolves, and when this authority lapsed, public devaluing of wolves reversed. Such volatile and responsive shifts in values would be an unprecedented scientific finding. Behaviours of individuals change quickly [10], but aggregate behavioural change sufficient to suppress wolf population growth would require highly synchronized changes in attitudes and norms relevant not only to outcomes of this behaviour (i.e. shared desirability of removal of wolves), but also to the act of engaging in illegal activity. Further, synchronized increase in poaching sufficient to suppress wolf population growth would require not only changing behavioural intent, but would also depend upon enough individuals encountering and acting upon opportunities to poach wolves broadly across both states. Research regarding Wisconsin citizens with wolf conflicts indicated that inclinations to poach wolves were highly contextual [11]. Therefore, even among those most motivated to poach wolves, not all feasible opportunities would be acted upon equally. Furthermore, Browne-Nunez *et al.* [11] found that intentions to poach wolves remained essentially unchanged during their study period (approx. 1 yr), which coincided with wolf delisting (i.e. LDM) and part of the 2012 Wisconsin wolf harvest. Thus, C&T’s assertion that liberalized culling leads to immediate devaluation of wolves and greater inclination to poach was not demonstrated [11]. Inference without adequate evidence of these behavioural dynamics is implausible.

C&T argued their results were applicable to public recreational hunting of wolves. Yet C&T only examined periods with agency culling (i.e. LDM) and did not present any analysis on potential effects of public hunting. In addition, they did not provide evidence that public attitudes of hunting and agency culling were similar. To the contrary, surveys done in both states have demonstrated that public acceptance of these types of killing is context-dependent and variable [12,13].

Growth of Wisconsin’s and Michigan’s wolf population has been decelerating in recent years and increased poaching probably is contributing [4,9]. C&T make strong assertions about mechanisms behind reduced growth based on a simple association with changes in policy and a biologically unrealistic model of expected growth. Inference from this association is far too weak to explain changes in illegal behaviours, which result from complex interactions of instrumental and normative influences. Yet C&T convey a level of certainty in the tone of their paper (e.g. the title, ‘... allowing culling increases poaching...’) that exceeds the quality of evidence and inference presented. C&T’s analysis fails to meet even Treves’s own gold or silver standards for scientific research on effectiveness of LDM [14].

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OLSON ET AL., FLAWED ANALYSIS AND UNCONVINCING INTERPRETATION: A COMMENT ON CHAPRON & TREVES 2016 - SUPPLEMENTAL MATERIAL

Evidence of negative density-dependence in North American wolves

Chapron and Treves (2016, hereafter C&T) tested for density-dependence using three life history parameters, and not at the more meaningful level of population growth rate, where additive and compensatory factors reconcile (Sibly 2003). Van Deelen (2009) compared the fit of exponential growth to a suite of six density-dependent models and found no support for exponential growth in Wisconsin and Michigan wolves through 2007. Recent analyses reaffirm these density-dependent patterns using data through wolf-year 2012 (Olson, *unpubl. data*). Van Deelen (2009) also observed that density-dependence coincided with regional saturation of high-quality habitat (Mladenoff et al. 2009; Olson, *unpubl. data*) and hypothesized that dispersal in sub-optimal habitat was a mechanism - a phenomenon Treves invoked in the context of dispersal patterns within the same book (Treves et al. 2009). The dispersal hypothesis was consistent with spatiotemporal patterns of mortality in a rigorous analysis of mortality estimated from radio collared wolves (Stenglein 2014) and was demonstrated plausible for Wisconsin wolves through simulations of a spatially-explicit individual-based model (Stenglein et al. 2015a; Stenglein and Van Deelen 2016). Negative density-dependence has also been observed for Yellowstone wolves, however, intraspecific strife was the likely mechanism (Stahler et al. 2013; Cubaynes et al. 2014; cf. Mech and Barber-Meyer). Negative density-dependence has been widely described for North American wolves using a variety of analytical techniques (Table S1).

Table S1. Papers reporting negative density-dependence in population growth or a component of population growth for wolves (*Canis lupus*) in North America

Citation	Location	Nature of evidence	Mechanism ^a
Hayes and Harestad 2000	Yukon, Canada	Yearly trends in growth rates and density	Competition for prey
Post et al. 2002	Isle Royale National Park, Michigan, USA	Growth model fit to annual population estimates	Not identified
Patterson and Murray 2008	Algonquin Provincial Park, Ontario, Canada	Growth model fit to annual population estimates, Regression of r_t on N_t^b	Not identified
Van Deelen 2009	Wisconsin and Michigan, USA	Growth Models fit annual population estimates	Not identified
Cariappa et al. 2011; (see also McRoberts & Mech 2014; Mech & Barber-Meyer 2015)	32 sites in North America	Statistical support for type 2 and 3 numerical responses in wolf density on prey biomass regressions	Intraspecific strife, territoriality, or something other than prey limitation
Stahler et al. 2013	Yellowstone National Park, Wyoming, USA	Regression analyses of demographic parameters on annual population estimates.	Intraspecific competition leading to reduced litter sizes and pup survival
Cubaynes et al. 2014	Yellowstone National Park, Wyoming USA	Capture-Recapture models fit to telemetry data	Social aggression leading to reduced adult survival at high density
Mech and Fieberg 2014	Isle Royale National Park (Michigan), Denali National Park (Alaska), Minnesota; USA	Growth Models fit annual population estimates	Not identified
Stenglein et al 2015a	Wisconsin, USA	Individual-based model parameterized with empirical data	Reduced mate-finding among dispersing wolves
Stenglein et al. 2015b	Wisconsin, USA	Integrated population model using annual population estimates & radio-telemetry data	Not identified
Stenglein and Van Deelen 2016	Wisconsin, USA	Individual-based model, Bayesian Penalized Splines	Dispersal interacting with Spatially structured mortality

^a Demonstrated or inferred; ^b $r_t = \ln(N_{t+1}/N_t)$; N = population estimate, t indexes time (years)

Evaluation of life history mechanisms and negative density-dependence

C&T claimed that "...poaching was the most parsimonious explanation for observed decreases in wolf population growth rates, because [they] could rule out alternative plausible biological explanations" (p.5). However, C&T evaluated only three life history features as potential component mechanisms for density-dependence: wolf pack reproduction, wolf pack size, and area occupied by wolf packs.

C&T estimated support for negative density-dependence using Bayesian techniques to evaluate slopes for linear relationships between each component and density. Imposing a rigid functional form of density-dependence (linear) precludes identification of more complex functional forms of negative density-dependence (Williams 2012; Stenglein and Van Deelen 2016). For example, area occupied by wolves in Wisconsin does demonstrate negative density-dependence (Stenglein and Van Deelen 2016; Olson, *unpubl. data*). Moreover, C&T's assumption that total area occupied is a sufficient representation of density-related effects on wolf territory size is not supported in the literature (Rich et al. 2012). Regardless, C&T may have failed to detect evidence of density-dependence for this variable because they only examined data from 2000 to 2011, when data are available as far back as 1980 for Wisconsin.

Also, C&T crudely estimated reproduction as a binary outcome (packs reproduce or not, yearly) and thereby failed to capture critical variation in litter size or pup survival (Brainerd et al. 2008; Stahler et al. 2013). C&T made *post hoc* estimates of reproductive performance using existing data (i.e., indirect estimates of changes in wolf pack size and presence of pups) (Chapron and Treves 2016). Such estimates would result in binary outcomes where pack reproduction is classified as *likely reproduced* or *undetected*, inadequate classifications for assessing density-dependence.

Additionally, these life history features are not a comprehensive set of alternate mechanisms that could contribute to negative density-dependent growth in wolves. Comprehensive mechanistic understanding of population growth may be impossible for species with complex life-histories living in variable environments; hence population biologists rely on growth as an integrator of interacting biotic and abiotic factors that influence vital rates (Sibly and Hone 2003). A demographic response to density (i.e. one observable in terms of population growth) is evidence of at least one instance of density-dependence in a component life history mechanism that influences growth (Berec et al. 2007). These components may not be identifiable with routine monitoring data and may interact in an additive or compensatory fashion (Berec et al. 2007). C&T's cursory examination of three potential components of growth cannot "eliminate alternative plausible biological interpretations." Thus, C&T fail to adequately account for negative density-dependence, which has been clearly documented for North American wolf populations, including those in Wisconsin and Michigan (Table 1).

Interpretation of social science literature

To support their inferences C&T challenge the frustration hypothesis (Olson et al. 2015a; Chapron and Treves 2016) stating, "Studies...have repeatedly shown that liberalized wolf killing did not reduce inclination to poach... [43, 44]," and "intentions [to poach wolves] rose in parallel with liberalized culling [44]..." (C&T's citation 43 and 44 refer to Browne-Nunez et al. 2015 and Treves et al. 2013). Treves et al. (2013) did find that inclination to illegally kill wolves increased from 2001 or 2003 to 2009, a period that coincidentally overlapped with highly inconsistent LDM authority (Chapron and Treves 2016, table s1). However, C&T's framing suggests the entire period was a period of liberalized culling, when in fact LDM was highly inconsistent (e.g., wolf status changed twice in 2009, Treves et al.'s [2013] comparison year).

Browne-Nunez et al. (2015) demonstrated that local people were frustrated with inconsistency in management and felt a lack of empowerment in dealing with wolves linked to the loss of LDM authority. Highly erratic LDM would likely influence attitudes or behavioral intentions differently than consistent LDM (Olson et al. 2015a).

C&T also state, "...and the penalties for wolf poaching did not change" (p.5) and cite Refsnider (2009) for support. This is misleading as well. Penalties for illegal killing of wolves changed with federal and state status of wolves. When wolves are listed as a federally endangered species the penalties are very substantial (Refsnider 2009), but decline drastically under state listing (Wisconsin DNR 1999). Furthermore, Refsnider (2009) makes no such statement. Enforcement against all illegal take of wolves has continued regardless of their legal status.

Parsimony

C&T argue that "...poaching was the most *parsimonious* explanation for observed decrease in wolf population growth rates..." (Chapron and Treves 2016, p.5, emphasis added) because of a "policy signal" generated by states' authority to conduct lethal depredation management (LDM). While a parsimonious hypothesis is not more valid simply on the basis of simplicity (truth can be complicated), parsimonious hypotheses benefit from shorter chains of inference. Longer chains of inference require more evidence supporting each additional link.

There are at least three non-exclusive hypotheses offered to explain recent reduced growth rates for wolves in the Southern Lake Superior Region (Figure 1). The first (density-dependence) is that negative density-dependence in vital rates caused reduction in growth as the wolf population increased. This hypothesis is supported by empirical data for Great Lakes wolves (Vucetich and Peterson 2004; Van Deelen 2009; Stenglein and Van Deelen 2016),

observations on the behavior of other colonizing or recovering populations (see earlier sections on density dependence) and is firmly grounded in ecological theory (Mills 2013).

The second hypothesis (frustration) is that local frustration with on-again, off-again authority for LDM coupled with increasing wolf numbers and increasing wolf depredations (Olson et al. 2015b) drove increased frustrations among stakeholders (Browne-Nunez et al. 2015) leading to increased poaching sufficient to cause population effects. This theory too has empirical support for a critical link (increasing frustration, sense of diminished empowerment among stake holders, increased negative attitudes, increased illegal killing) (Treves et al. 2013; Browne-Nunez et al. 2015; Olson et al. 2015a). However, the second intermediate link has not been established (figure 1): there is no evidence that increased poaching during the time series exceeded compensatory mechanisms and reduced growth. Compensation for a given source of mortality increases with population density (Kautz 1990; Péron 2013) and C&T's finding that population growth was unrelated to the actual number of wolves killed through LDM, despite an informative Bayesian prior essentially enforcing super-additivity, is consistent with high compensation for human-caused mortality. Analysis of radio-collared wolves indicated that rates of poaching and other human-caused mortality were highly variable and generally increasing during 1995-2012 while rates of natural mortality generally decreased in a manner consistent with compensation (Stenglein 2014). A plausible variation of the frustration hypothesis is that human-caused mortality (poaching and non-poaching) may itself be a density-dependent component of growth and this mechanism was clearly operating prior to C&T's putative policy signal (Olson et al. 2015a).

The third hypothesis (devaluing, Chapron and Treves 2016) asserts that initiation of LDM, apart from its actual implementation, devalued wolves sufficiently among would-be

poachers such that poaching increased enough to exert population effects. This chain has an additional link unsupported by empirical evidence. There are no measures of changes in valuation of wolves in the Great Lakes region concurrent with policy changes. C&T suggested that implementing LDM produced a “policy signal” or “a negative message about the value of wolves or that poaching prohibitions would not be enforced” (p. 5). Yet, even intentional, clearly communicated policy changes rarely produce such immediate and clear behavioral responses among stakeholders (Triezenberg et al. 2016). It is reasonable to assume a “policy signal” could result in a misguided public interpretation of lax enforcement policy. It is not reasonable to assume subsequent changes in poaching behavior would be strong enough and fast enough to suppress population growth when clearly targeted communications campaigns encouraging legal harvest under liberal regulations fail to produce even modest increases in harvest (Triezenberg et al. 2016). C&T proposed that psychological theory of hazard assessment may explain how poaching behavior was influenced, and C&T cite a planned communication experiment in which failure to communicate information about and benefits of bears led to diminished public acceptance (Slagle et al. 2013). C&T provide no explanation for why direct and intentional communications campaigns regarding benefits of bears produced only a small change in attitudes towards bears (Slagle et al. 2013), and yet, indirect, unintentional, and informal “signals” of implied changes in enforcement policy or diminished value of wolves would produce such a strong behavioral response (i.e., poaching with population effects).

Of these three hypotheses, the chain of inference is shortest for the density dependence hypothesis, which also accommodates the frustration hypothesis if one allows that frustration-driven human-caused mortality (Olson et al. 2015a) can be a component mechanism. The chain of inference for the devaluing hypothesis (Chapron and Treves 2016) is longest and

indistinguishable from the frustration hypothesis without convincing evaluation of key intermediate links. C&T dismiss the frustration hypothesis, arguing that frustration with wolf management was present prior to LDM authority (p. 5). But there is no evidence that devaluation of wolves was exclusive to the period after implementation of LDM. Similarly, poaching has always been a feature of the population biology of Great Lakes wolves and occurred at higher rates prior to 1985 when wolves were fully protected and there was no “policy signal” (Stenglein 2014). In truth, general frustration with wolf management probably correlates with devaluing of wolves despite C&T’s assertion that devaluing depends on a specific and discrete outcome of changing policy. Hence it makes no sense to justify the devaluing hypothesis on the basis of parsimony.

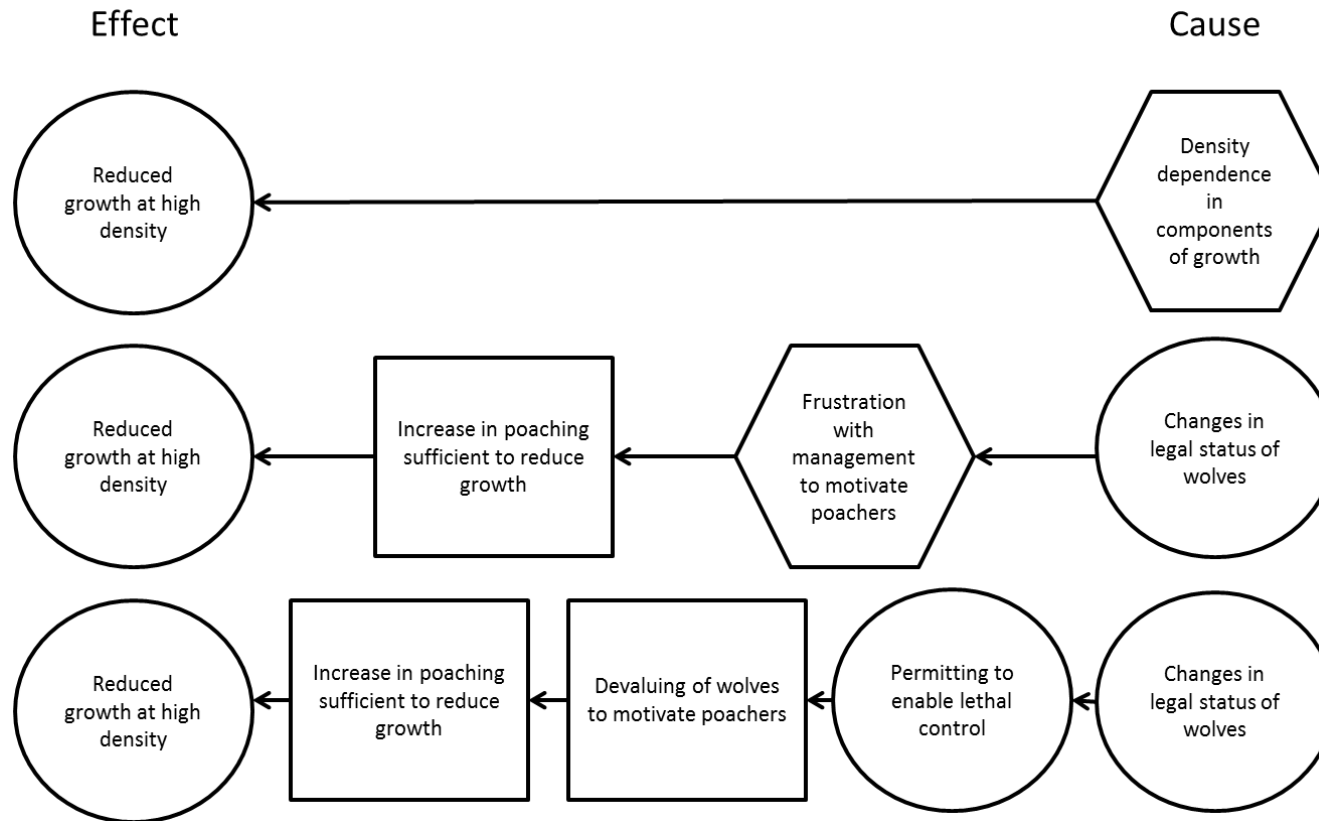


Figure 1. Schematic representation of chains of inference needed to support 3 hypotheses to explain observations of reduced population growth in Great Lakes wolves 1995-2012. Hypotheses are 1) Density dependence (top), Frustration (middle) and Devaluation (bottom, see text for a fuller explanation). Links that are fully observed are represented as circles. Links that have been demonstrated from empirical data and have strong theoretical support are represented as hexagons. Links that have not been demonstrated from empirical analysis or have limited theoretical support are illustrated as rectangles.

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