

Holling Meets Habitat Selection - Functional Response of Large Herbivores Revisited

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Keywords: discrete choice, herbivore, landscape complementation, landscape of fear, mixed effects, multinomial, ungulate

Posted Date: February 18th, 2021

DOI: <https://doi.org/10.21203/rs.3.rs-208563/v1>

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Version of Record: A version of this preprint was published at Movement Ecology on September 6th, 2021. See the published version at <https://doi.org/10.1186/s40462-021-00282-6>.

Abstract

Background: Holling (1959) was the first to describe a functional response between a predator's consumption-rate and the density of its prey. The same concept may be applied to the habitat selection of herbivores, by considering the change in relative habitat use with the change in habitat availability. Functional responses in habitat selection at a home-range scale has been reported for several large herbivores. However, a link to Holling's original functional response types has never been drawn despite its potential to understand availability dependence in habitat selection more profoundly.

Methods: Discrete choice models were implemented as mixed-effects baseline-category logit models to analyze the variation in habitat selection of a large herbivore over seasonal and diurnal scales. Specifically, changes in habitat use with respect to habitat availability were investigated by monitoring 11 habitat types commonly used by roe deer (*Capreolus capreolus*) in the Bavarian Forest National Park, Germany. Functional response curves were then fitted using Holling's formulas.

Results: Strong evidence of non-linear functional responses was obtained for almost all of the examined habitat types. The shape of the functional response curves varied depending on the season, time of day and in some cases between sexes. These responses could be referenced to Holling's types, with a predominance of type II.

Conclusions: Our results indicate that Holling's types could be applied to describe general patterns in habitat selection behaviour of herbivores. Functional response in habitat selection may occur in situations of trade-off in the selection of habitats offering different resources, due to temporally varying physiological needs of herbivores. Moreover, the two associated parameters defining the curves helps to identify the temporal variations and clarify how strongly the cost-to-benefit ratio is pronounced for a specific habitat. The presented novel approach of using Holling's equations to describe functional response in habitat selection of herbivores could be used for assigning general habitat attraction values, independent of habitat availability, which might facilitate the identification of suitable habitats.

Full Text

Due to technical limitations, full-text HTML conversion of this manuscript could not be completed. However, the latest manuscript can be downloaded and [accessed as a PDF](#).

Figures

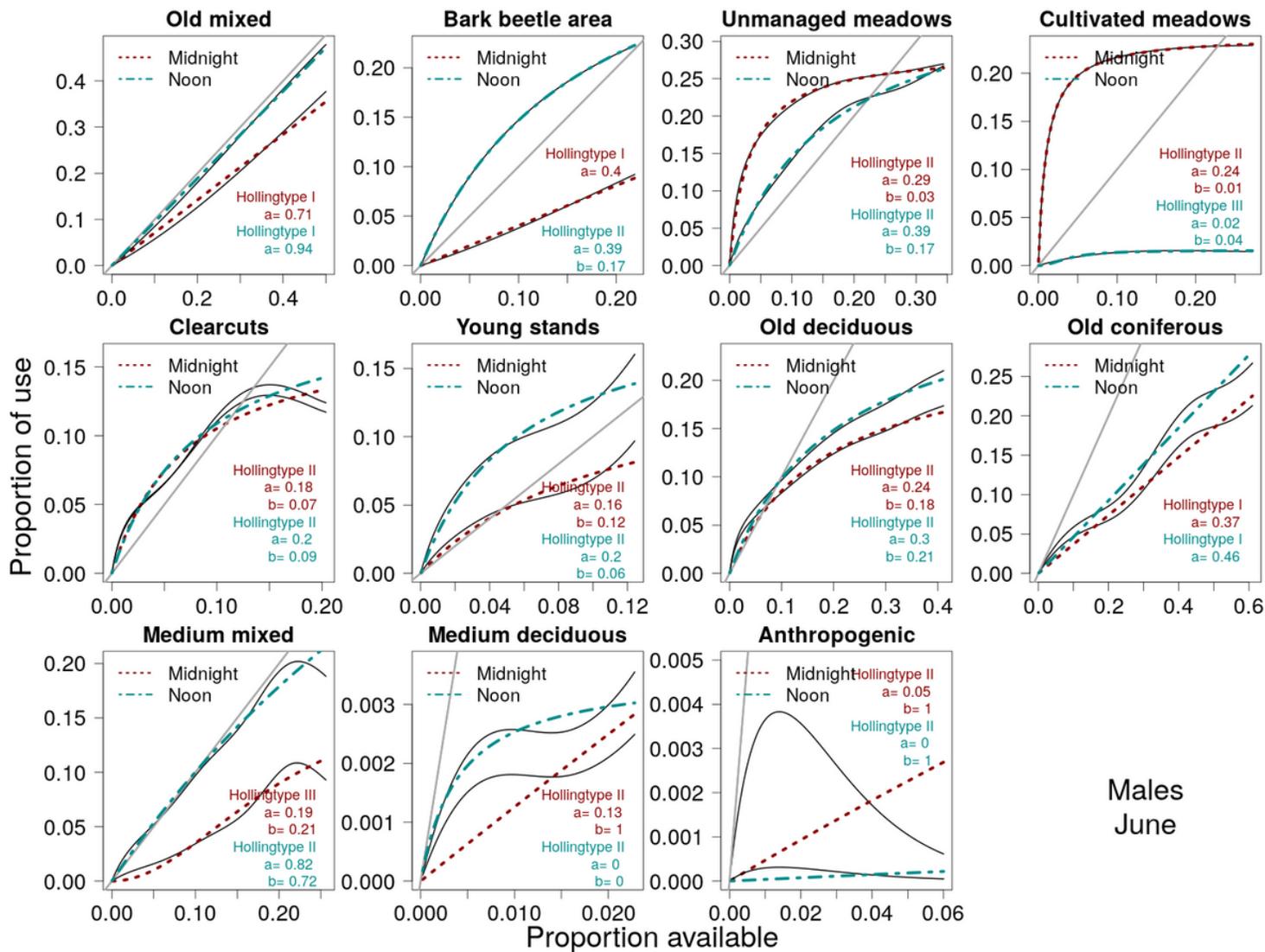


Figure 1

Shapes of functional response curves based on Holling's types I, II or III for all habitats in June for 19 males roe deer during night (red dashed line) and day (green dot-dashed line) and the associated estimated optimal values for the parameters defining the Holling type. Black lines in the background of the coloured curves are the estimates based on multicategory logit models. Grey line indicates proportionality of use to availability.

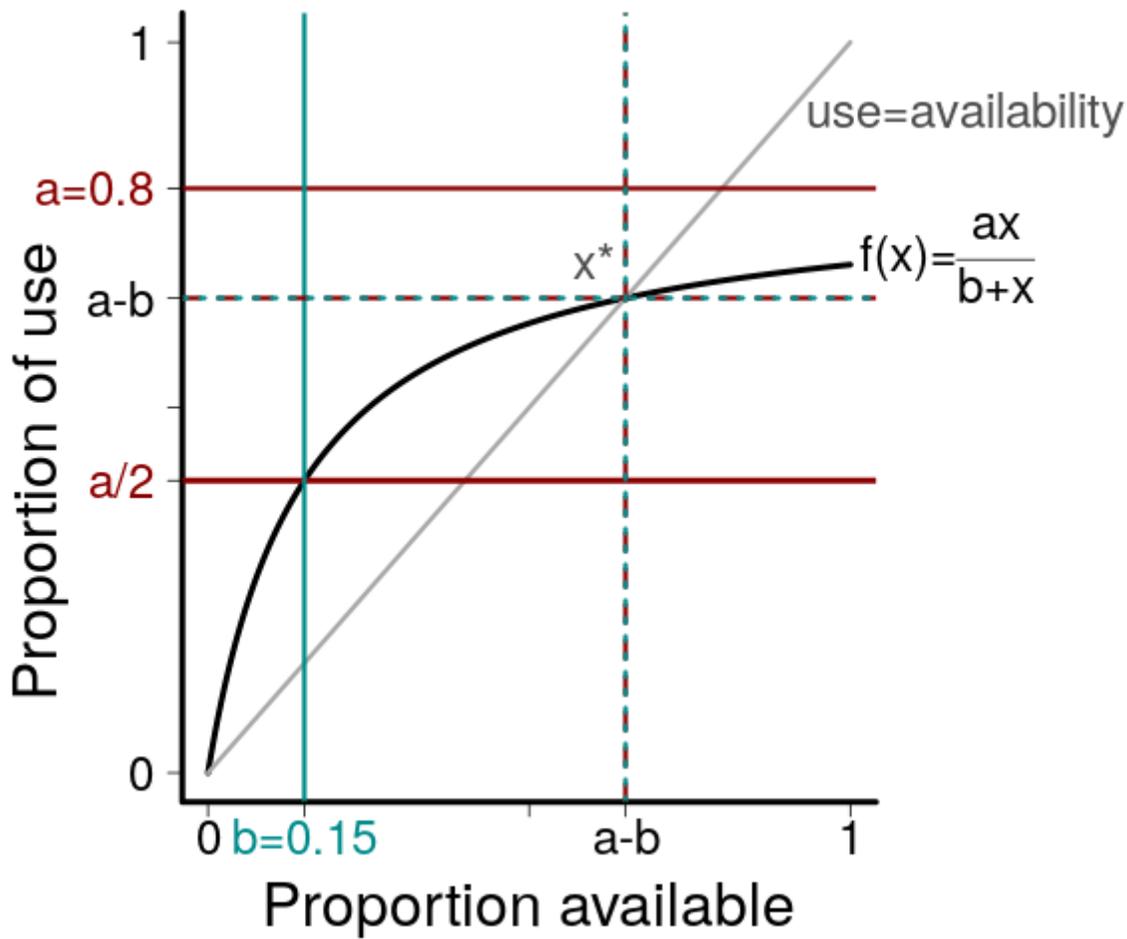


Figure 2

Concept plot of the most familiar Holling's type II functional response $y(x) = \frac{ax}{b+x}$ for $a = 0.8$ and $b=0.15$. x is the proportion of availability of a habitat in the home range, limited between 0 and 1, $f(x)$ is the use of a habitat limited between 0 and a , the upper bound of use and b the availability of a habitat at which the habitat is used half of the maximum ($f(b) = a/2$). Parameters a and b become ecologically valuable and interpretable when applying limit calculations (see Appendix S2, S10).

Supplementary Files

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- [Appendixfctresponse.pdf](#)
- [FunResp vignette.html](#)