Wildlife species diversity in Oli Complex of Kainji Lake National Park, Nigeria

Olajesu, S. O.1*, Oni, F. L¹. and Olubode, O. S.²

¹Department of Wildlife & Ecotourism Management, Faculty of Renewable Natural Resources, University of Ibadan, Ibadan. Nigeria

²Department of Crop Protection and Environmental Biology, Faculty of Agriculture, University of Ibadan,

Ibadan. Nigeria

*Corresponding Author: taioladipo@gmail.com, +234 807 527 0516

Abstract

The survey of wildlife species diversity is important for management and decision making in Wildlife Parks in order to achieve effective conservation. Up-to-date information on the diverse fauna species in Kainji Lake National Park is scarce. Therefore, wild animal species diversity in the National Park was assessed. The line transect and total enumeration count methods were used in the study. Oli Complex was stratified into five line transects laid at 5 km intervals and then a census of wild animals was taken following standard procedures. Data were analyzed using descriptive and inferential statistics. Fifty-nine taxa were identified with 4,665 individuals enumerated. A total of 24 Mammalia, 24 Avifauna, 8 Reptilia, 1 Amphibia and 2 Mollusca species were identified. Buffon's kob (Kobus kob kob) was the most abundant (2,019), followed by the Olive baboon (Papio anubis) (963), helmeted Guinea fowl (Numidea melagris) (189) and Red Flanked (RF) duiker (Cephalophus rufilatus) (118). Dominance was low (0.2) with high diversity index (0.8), low evenness (0.2); that was moderately spread but not equally (0.6) distributed within the study area. Buffon's kob had the highest relative importance index (24.13%), while Guinea fowl had the least (3.27%). Buffon's kob had the highest density (40.38/ km²), followed by Olive baboon (19.26/km²), Guinea fowl (3.78/km²), Roan antelope (3.32/ km²) and Red Flanked duiker (2.36/ km²). Oli Complex of Kainji Lake National Park had a high wildlife diversity and supported a wide range of animal species. Keywords: Abundance; Density; Dominance; Species Index; Oli Complex

Introduction

Wild animal species diversity is an important aspect of biodiversity management focusing on the array of animals on land, water and in the air. The diversity of wildlife, regardless of their habitats, depend on both abiotic and biotic factors. The abiotic factors that influence fauna include soil, air, and water quality; while biotic factors include: the availability of plant and animals they depend on. Anthropogenic factors such as hunting, pollution and other forms of disturbance also play important roles in animal diversity. Hence, animal diversity or

population may increase or decrease conditional, based on the quality of these variables and the level of human intrusion (Abere and Lateef, 2015; Olajesu *et al.*, 2019).

Fauna distribution across different habitats may be uneven or dense. In most cases, areas with dense animal population are expected to be safe from poaching. For instance, a permanent waterhole with competition moderate and predation (Fryxell et al., 2004; Rduch, 2013). Unfortunately, in Nigerian National Parks, problems such as poaching, habitat logging, encroachment, fishing, unsustainable agricultural practices,

constrain wild animal diversity (Lameed, 2007).

Conservation of wildlife in National Parks through sustainable management is essential for biodiversity management and preservation of genetic resources (Reid, Consequently, 2001). effective management of Parks play significant roles in ensuring the continuous presence of animals for conservation and touristic benefits. However, most Parks in Nigeria have challenges with monitoring and documentation of the current status of resident wildlife, due to poor funding, inadequate infrastructure, weak legislation, maladministration, limited logistics. corruption and other administrative lapses (Dore, 2001; Amusa, 2003). There is need for regular updating of the checklist of wild animals to ensure proper management, effective monitoring and increased availability of resources to potential tourists. Therefore, this study determined the fauna species diversity and index of Oli Complex in Kainji Lake National Park (KLNP).

Materials and Methods

Study Area

Kainji Lake National Park is situated in Kwara and Niger states (Latitude 9° 50' 19" N and Longitude 4° 34' 24" E) of Nigeria. It is the second largest protected area (5,340.82 km²) in Nigeria and consist of two sectors (Figure 1): a larger area called the Borgu sector (3,970.02 km²), and a smaller area known as Zugurma sector (1,370.80 km²) (Marguba, 2002). This research was limited to Oli Complex (Figure 2) of the Borgu sector in Niger State. Wet and dry seasons are the major climatic features of the Park. The wet season starts from May and runs through November while the dry season is observed from December to April. Annual rainfall ranges from 1100 mm - 1150 mm. The Borgu sector has a transitional vegetation between the Sudan and Northern Guinea Savanna.

Data Collection

Global Positioning System was used to locate five transects of 5 km length and 100 m width. Total Enumeration Count (TEC) was employed to enumerate fauna species along the five transects, twice daily (morning: 07.00 - 10.00 hours; and evening: 15.00 – 18.00 hours, respectively). The Oli Complex was stratified into five based on existing Jeep tracks, namely; Gilbert Child (GC), Shehu Shagari (SH), Hussein Mashi (HM), Mamudu Lapai (ML), and Mara Tsuade (MT). This census was carried out for two years (2012-2014) during the dry (December – March) and wet (June – September) seasons. The TEC was limited to a stratum for each day of the week for effectiveness and accuracy, while limiting the degree of error. The number and types of fauna species encountered was recorded and pooled, at the end of the study. Observation on each transect followed standard procedures, a manual counter and a 10 x 40 mm binoculars was used to enhance counting and observation.

Data Analysis

Data obtained were analysed using descriptive statistics (frequency, percentages) and inferential statistics. Quantitative data on fauna abundance were subjected to multivariate analyses using Paleontological Statistics (PAST Version 3.13), following the method of Hammer *et al.* (2016). Specifically, the data were

subjected to ordination by Detrended Correspondence Analysis (DCA) and Principal Component Analysis (PCA). Species associations were assessed with cluster analysis using Euclidean Distance as Coefficient of Association.



Figure 1. Map of Borgu and Zugurma Sectors in Kainji Lake National Park (inset: Map of Nigeria) (Source: Lateef and Lameed, 2018)



Figure 2. Map of Oli Complex in Kainji Lake National Park Source: Olajesu *et al.* (2019)

Results

A total of 24 Mammalia, 24 Avifauna, 8 Reptilia, 1 Amphibia and 2 Mollusca species were observed. Buffon's kob (*Kobus kob*) had the highest (2,019) abundance (Table 1). Other species with high abundance included: Olive baboon (*Papio anubis*) (963), Helmeted Guinea fowl (*Numidia meleagris*) (189) and Red Flanked duiker (*Cephalophus rufilatus*) (118). The least abundance was recorded for avifauna (hawk and hoepoe), African giant snail and snakes (Table 1).

The alpha species indices of wildlife encountered in Oli Complex of KLNP were presented in Table 2. A total of fifty-nine (59) taxa were identified with 4,665 individuals enumerated. Dominance was very low (0.2), but Simpson diversity index was high (0.8). The degree of evenness was very low (0.2), though moderately spread but not equally (0.6) distributed within the study area. In addition, dormancy was very low (0.2), such that no fauna species dominated the Complex. Thus, moderate equitability (0.5) existed among the fauna species within the Oli Complex (Table 2).

Buffon's kob had the highest relative importance value (24.1%), followed by Olive baboon (12.8%). Others were: Roan antelope (4.0%), Red flanked duiker (3.6%) and Guinea fowl (3.2%) (Table 3). *Archatina* spp., *Python* spp., *Naja* spp. and bird species such as *Kaupifalco* spp., *Polyboroides* spp., *Upupa* spp. were rare in Oli Complex (Table 3).

The dissimilarity of fauna relationship at Oli Complex of KNLP was separated by Euclidean Distance over 600 points (representing 100%). At the maximum dissimilarity (600), there were two main fauna groups. *Kobus kob* population had a distinct group, while the remaining fauna populations formed the second group. At 50% dissimilarity rating (300), three groups were determined, comprising *Kobus kob*, *Papio anubis*, and the others. At approximately 10% (66), eight clusters were determined, comprising *Kobus kob* population, Guinea fowl, *Hippopotamus equinus*, small birds, snails and the remaining fauna population (Figure 3).

Ordination of Plots and Fauna Species at Oli Complex

Principal components 1 and 2 depicted the fauna species to be mainly determined by Plots T2R1, T4D1, T1R1 on the positive side of Principal component 1, while Plot T2D2 was the main plot on the other side (Figure 4). *Papio anubis* was the only outlier on the positive side, while *Kobus kob* was the outlier on the other side, where T2D2 was the main determining plot (Figure 4). The DCA biplot of the species and plots further indicated plots T5D2, T3R2, T3D2 and T3D1 as outliers outside the border of 95% Eclipse (Confidence Interval) (Figure 5).

Table 2. Alpha species indices ofenumerated wildlife in Oli Complex ofKainji Lake National Park

Таха	59
Individuals	4665
Dominance	0.24
Simpsons	0.76
Shannon Wiener	2.28
Evenness	0.17
Brillouin	2.26
Menhinick	0.86
Margalef	6.87
Equitability	0.56
Fisher alpha	9.55
Berger-Park	0.43

S/N	Species	ecies Common Name	
1	Kobus kob	Buffon's kob	2,019
2	Papio Anubis	Olive baboon	963
3.	Hippotragus equinus	Roan antelope	166
4.	Cephalophus rufilatus	Red flanked (RF) duiker	118
5.	Numida meleagris	Helmeted guinea fowl	189
6.	Tragelaphus scriptus	Bushbuck	76
7.	Xerus erythropus	Ground squirrel	52
8.	Tockus nasutus	Grey hornbill	88
9.	Civettictis civetta	African Civet cat	70
10.	Hystrix africanus	Brush-tailed Porcupine	36
11.	Francolinus bicalcaratus	Partridge	66
12.	Cercopithecus aethiops	Green monkey	52
13.	Porcochoerus aethiopieus	Warthog	48
14.	Cinnyris venustus	Sunbirds	46
15.	Bucorvus abyssinicus	Ground hornbill	29
16.	Caracal caracal	Caracal cat	29
17.	Thryononyms swinderianus	Grasscutter	30
18.	Coturnix ypsilophoraf	Bush fowl	39
19.	Felis serval	Serval	38
20.	Alcelaphus buselaphus	Western hartebeest	35
21.	Cercopithecus mona	Mona monkey	34
22.	Streptopelia senegalensis	Laughing dove	41
23.	Hirunda abyssinica	Striped swallow	57
24.	Veranus niloticus	Monitor lizard	19
25.	Phalacrocorax africanus	Longtail shag	17
26.	Hippopotamus amphibious	Hippopotamus	16
27.	Genetta genetta	Genet cat	24
28.	Ploceus cucullatus	village weaver	70
29.	Francolinus ptilopachus	Francolin	22
30.	Python sebae	Python	8
31.	Halcyon senegalensis	Woodland kingfisher	6
32.	Bitis arietans	Puff adder	17
33.	Centropus senegalensis	Senegal coucal	11
34.	Sylvicapra grimmia	Grimm's duiker	9
35.	Syncerus caffer	Buffalo	8
36.	Redunca redunca	Reedbuck	25
37.	Poicephalus senegalus	Senegal parrot	12
38.	Kinixys belliana	Hinged-back tortoise	7
39.	Panthera leo	Lion	6
40.	Myomys daltoni	Bush mouse	6
41.	Motacilla flava	Yellow wagtail	3
42.	Crocodilus niloticus	Nile crocodile	4
43.	Milvus migrans	Yellow billed kite	15
44.	Ardea cinereal	Grey Heroin	6

Table 1a. Abundance of fauna species encountered in Oli Complex of Borgu Sector in Kainji Lake National Park

S/N	Species	Common Name	Abundance	
45.	Corythaeola cristata	blue bird	4	
46.	Naja nigricoli	Spitting Cobra	4	
47.	Sagittarius serpentarius	Secretary bird	1	
48.	Hyperolius viridiflavus	Common reed frog	1	
49.	Crossarchus obscurus	Mongoose	10	
50.	Erythrocebus patas	Patas monkey	2	
51.	Hirunda smithii	wire tailed swallow	2	
52.	Alcedo cristata	malachite kingfisher	2	
53.	Archachatina maginata	Giant Snail	1	
54.	Kaupifalco monogrammicus	Lizard buzzard	1	
55.	Archatina fulica	African giant snail	1	
56.	Python regis	Royal python	1	
57.	Polyboroides typus	Harrier hawk	1	
58.	Upupa epops	Hoepoe	1	
59.	Naja melanoleuca	Black cobra	1	

Table 1b. Abundance of fauna species encountered in Oli Complex of Borgu Sector in Kainji Lake National Park



Figure 3: Dendogram of relationships among fauna species of Oli Complex in Kainji Lake National Park

S/N	Species	RIV	D	RD	F	RF
1.	Kobus kob	24.13	40.38	43.28	20	4.98
2.	Papio Anubis	10.01	10.26	20.64	20	4.98
3.	Hippotragus equinus	12.81	19.20	20.04	20	4.48
4	Canhalonhus rufilatus	4.02	3.32	3.56	18	1 73
4.	Cephalophus Tujilalus	3.63	2.36	2.53	19	4.75
5.	Numida meleagris	3.27	3.78	4.06	10	2.49
6.	Tragelaphus scriptus	2.93	1.52	1.63	17	4.23
7.	Xerus erythropus	2.80	1.04	1.11	18	4.48
8.	Tockus nasutus	2.68	1.76	1.89	14	3.48
9.	Civettictis civetta	2.37	1.4	1.50	13	3.23
10.	Hystrix cristata	2.25	0.72	0.77	15	3.73
11.	Francolinus bicalcaratus	2.08	1.32	1.41	11	2.74
12.	Cercopithecus aethiops	1.93	1.04	1 11	11	2.74
13.	Parcochoerus aethiopieus	1.95	0.06	1.11	11	2.74
14.	Cinnyris venustus	1.00	0.90	0.00	11	2.74
15.	, Bucorvus abyssinicus	1.00	0.92	0.99	11	2.99
16	Caracal caracal	1.80	0.58	0.62	12	2 49
17	Thruchomus swinderignus	1.55	0.58	0.62	10	2.12
17.		1.44	0.6	0.64	9	1.00
18.	Coturmix ypsilophora	1.41	0.78	0.84	8	1.99
19. 20	Felis serval	1.40	0.76	0.81	8	1.99
20.	Alcelaphus buselaphus	1.37	0.7	0.75	8	1.99
21.	Cercopithecus spp	1.36	0.68	0.73	8	1.99
22.	Streptopelia senegalensis	1.31	0.82	0.88	7	1.74
23.	Hirunda abyssinica	1.23	1.14	1.22	5	1.24
24.	Veranus niloticus	1.20	0.38	0.41	8	1.99
25.	Phalacrocorax africanus	1.18	0.34	0.36	8	1.99
26.	Hippopotamus amphibious	1.17	0.32	0.34	8	1.99
27.	Genetta tigris	1.00	0.48	0.51	6	1.49
28.	Ploceus cucullatus	1.00	1.4	1.50	2	0.50
29.	Francolinus ptilopachus	0.08	0.44	0.47	6	1.49
30.	Python sebae	0.90	0.14	0.47	0 C	1.49
31	Halevon senegalensis	0.83	0.16	0.17	6	1 /19
51.	nucyon seneguiensis	0.81	0.12	0.13	6	1.47
32.	Bitis arietans	0.80	0.34	0.36	5	1.24

Table 3a. Relative importance value, density and relative frequency of fauna species inOli Complex of Kainji Lake National Park

KEY: RIV = Relative Importance Values; RD = Relative Density; RF = Relative Frequency; D=Density/1000km² and F = Frequency

33.	Centropus senegalensis	0.74	0.22	0.24	5	1.24
34	Sylvicapra grimmia	0.72	0.18	0.19	5	1.24
35.	Syncerus caffer	0.71	0.16	0.17	5	1.24
36.	Redunca redunca	0.64	0.5	0.54	3	0.75
37.	Poicephalus senegalensis	0.63	0.24	0.26	4	1.00
38.	Kinixys belliana	0.57	0.14	0.15	4	1.00
39.	Panthera leo	0.56	0.12	0.13	4	1.00
40.	Myomys daltoni	0.56	0.12	0.13	4	1.00
41.	Motacilla flava	0.53	0.06	0.06	4	1.00
42.	Crocodilus niloticus	0.42	0.08	0.09	3	0.75
43.	Milvus migrans	0.41	0.3	0.32	2	0.50
44.	Ardea cinereal	0.31	0.12	0.13	2	0.50
45.	Corythaeola cristate	0.29	0.08	0.09	2	0.50
46.	Naja nigricoli	0.29	0.08	0.09	$\frac{1}{2}$	0.501
47.	Sagittarius serpentarius	0.26	0.02	0.02	2	0.50
48.	Hyperolius vividigulasus	0.26	0.02	0.02	2	0.50
49.	Crossanclus obscurus	0.23	0.2	0.21	1	0.25
50.	Erythrocebus patas	0.15	0.04	0.04	1	0.25
51.	Hirunda smithni	0.15	0.04	0.04	1	0.25
52.	Alcedo cristata	0.15	0.04	0.04	1	0.25
53.	Archachatina marginata	0.14	0.02	0.02	1	0.25
54.	Kaupifelco monogrammicus	0.14	0.02	0.02	1	0.25
55.	Archachatina fulica	0.14	0.02	0.02	1	0.25
56.	Python regis	0.14	0.02	0.02	1	0.25
57.	Polyboroides typus	0.14	0.02	0.02	1	0.25
58.	Upupa epops	0.14	0.02	0.02	1	0.25
59.	Naja melanoleua	0.14	0.02	0.02	1	0.25

 Table 3b. Relative Importance Value, Density and Relative factors of fauna species in Oli

 Complex of Kainji Lake National Park

KEY: RIV = Relative Importance Values; RD = Relative Density; RF = Relative Frequency; D=Density/1000km² and F = Frequency 🥔 PCA scatter diagram



Figure 4. Principal component analysis biplots of fauna species and plot ordination in Oli Complex of Kainji Lake National Park



Figure 5. Detrended correspondence analysis biplots of fauna species and plot ordination in Oli Complex, Kainji Lake National Park

Discussion

Oli Complex had a high wildlife species diversity and supported an abundant fauna species population. Buffon's kob had the highest relative importance value (24.13%), while eight other antelope species, birds, reptiles, amphibians and molluscs were identified. This is an indication that the Complex is an important fortress for wildlife resources in Kainji Lake National Park (KLNP). It is a vital tourist centre in the Park and should be given adequate protection. Halidu et al. (2013) mentioned that Oli River was the major perennial water source in the Borgu Sector of KLNP, with large congregations of wild animals particularly, during dry season. The high number of species from the mammalian class may be an indication of the Guinea Savanna region which has sparsely distributed trees and high availability of food. On the other hand, the low presence of amphibians and molluscs may be due to the aridity and high temperature of the region. With the abundance of wild animals observed, Oli Complex is a hotspot that must be conserved, especially with the large number of kobs and baboons in the sector (East et al., 1988; Meduna et al., 2008).

Unfortunately, the National Park Service and KLNP management are facing serious challenges with declining species diversity in the Complex and other ranges. These challenges emanate from problems such as, deforestation, fragmentation, habitat competition and herdsmen invasion of KLNP. Presently, Oli Complex, has the highest species diversity among ranges, with other ranges losing animals, especially kobs, to poaching and other factors. One of the causal factor emphasized by Lameed (2007) was the widespread poverty forcing rural communities, in close proximity to the

Park, to encroach into the buffer zones for farming and rearing of domestic animals. Climate change has also been identified as a possible indirect factor influencing the increasing encroachment of the Park by the rural communities (Lateef and Lameed, 2018). Rapid population growth is further causing deforestation at an alarming rate in Nigeria. These is depleting the available habitats and safe havens for wild animals (Iroye, 2010).

Species dominance was low between and within groups, with no group having prevalence on others in Oli Complex. There were 59 taxa, moderately spread across the site. The density of kobs was 2.32 kobs/km². They were the most abundant (43%) and most commonly sighted (60%) species in the Park. This large population of kobs, (the flagship species of Kainji National Park) confirmed the fact that they have evolved to make efficient use of the resources available in Northern Guinea Savanna (Alawode et al., 2017; Fingesi et al., 2019). The findings agree with Taiga et al. (2019), who made a similar observation of high kob abundance in Faro National Park in the Northern Cameroon; which has similar vegetation with Kainji National Park in Nigeria.

Kobs, Olive baboons and Guinea fowls were distinctly dominant species with large populations that minimally associated with the populations of other fauna species. The other fauna species interacted more at lower levels of association. The dissimilarity in the associations of Kobs, Baboons and Guinea fowls might be due to disparate food preferences, which make them to be unlikely competitors for resources. Hence, wildlife management strategies in KLNP should focus on keystone species, especially kobs and baboons, as well as other fauna species that contribute to the population diversity of wildlife in Kainji Lake National Park in Nigeria.

Conclusion

Oli complex of Kainji Lake National Park was found to be rich in diverse fauna species. Antelope species were the most abundant while amphibians and molluscs

References

Abere S. A. and Lateef F. L. (2015). A conference proceeding of African Society of Agronomy, Crop, Soil and Environmental Sciences. 2-5 November, 2015. Pp 250-262.

Alawode, S. O., Lateef, F. L. and Lameed, G. A. (2017): Population structure and distribution of Buffon's kob (*Kobus kob kob*) within Oli Complex in Kainji Lake National Park, Nigeria International Journal of Scientific and Engineering Research (8) 1643- 1655.

Amusa, T. O. (2003): Why the conservation of wildlife is important to Nigeria. *The Nigerian Field* 69: 32-40.

Dore, M. P. O. (2001): Wildlife Consumption and Biodiversity Conservation. *Nigerian Journal of Forestry* Vol. 31 (1and2): July, 2001 Pp 94-99.

East, R., Grubb, P. and Wilson, V. J. (1988): Classification of antelopes adopted for the antelope survey. In: East, R. (Compiler) Antelope global survey and regional action plan Part 1: East and Northeast Africa.

Fingesi, U. I., Orsar, T. J., Egwumah, P. O. and Tyowua, B. T. (2019): Abundance and distribution of Kobs (*Kobus kob kob*, Erxleben, 1777) in Kainji Lake National Park, Nigeria. World Scientific News were least. Most of the species were clustered around Oli complex and their population decreased with movement away from the complex, suggesting that poaching activities might be higher in other ranges. This, therefore, calls for urgent, effective and sustainable action to safeguard animal diversity and abundance in the Park

(WSN) 138 (2) 260-276 EISSN2392-2192 @www.worldscientificnews.com.

Fryxell, J. M., Wilmshurst, J. F., and Sinclaire, A. R. E. (2004): Predictive models of movement by Serengeti grazers. *Ecology* 85: 2429-2435.

Halidu, S. K., Ayodele, I. A., Lameed, G. A. and Oyeleye, D. A. (2013). Seasonal and daily distribution pattern of selected antelopes in relation to water hole utilisation in Kainji Lake National Park, Nigeria. *Journal of Forestry Research and Management* 10: 52-66.

Iroye, K. A. (2010). Deforestation and sustainable watershed management in Nigeria: A reflection. *Environmental Issues* 3 (1): 74-81.

Lameed, G. A. (2007). Kainji Lake National Park of Nigeria: Assets and implications for sustainable development. *Biodiversity* 8(4): 3-13.

Lateef F. L and Lameed G. A. (2018). Effects of a changing climate on the sustainable management of Wildlife in Kainji Lake National Park. Proceedings of the 2nd Wildlife Society of Nigeria Conference held from 16th - 19th September, 2018. Pp. 250-258. Marguba, L. B. (2002): National Parks and their benefits to local communities in Nigeria. Nigerian National Park Service. 34pp.

Meduna, A. J., Oyeleke, O. O., Amusa, T.O., Likita, I. B., Ajayi, S. R., Akor, S. and Patrick, V. (2008). Evaluation of Kob (*Kobus kob* Erxleben) habitat in KLNP, Nigeria. *Obeche Journal* 26 (1): 40-44.

Olajesu S. O., Akinyemi F. O., Lateef F. L and Lameed G. A (2019). Population density, diversity and abundance of antelope species in Kainji Lake National Park, Nigeria. *Open Journal of Ecology* 9: 107-116.

https://doi.org/10.4236/oje.2019.94009

Reid, H. (2001). Contractual National Parks and the Makuleke Community. *Human Ecology* 29(2):135-155.

Rduch V. (2013). Ecology and population status of the Puku antelope (*Kobus vardonii* Livingstone 1857) in Zambia. Dissertation for the degree of Doctor of Science in Zoology at the Rheinische Friedrich-Wilhelms-Universität Bonn.

Taiga, L. K, Kumgana, S. A., Fils, E. M.
B., Samuel, T. C. and Rduch, V. (2020).
The status and population dynamics of
Buffon's kob (*Kobus kob kob*, Erxleben, 1777) in the Faro National Park, Northern
Cameroon. *African Journal of Ecology* 59: (1) 1-10. doi: 10.1111/aje12808.