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Summer habitat use and movements of invasive wild pigs (*Sus scrofa*) in Canadian agro-ecosystems

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Abstract

Resource selection informs understanding of a species' ecology and is especially pertinent for invasive species. Since introduced to Canada, wild pigs (*Sus scrofa* Linnaeus, 1978) remain understudied despite recognized negative impacts on native and agricultural systems globally. Elsewhere in North America, pigs typically use forests and forage in agricultural crops. We hypothesized Canadian wild pigs would behave similarly, and using GPS locations from 15 individuals, we examined diel and seasonal resource selection and movement in the Canadian prairie region. Forests were predominately selected during the day, while corn (*Zea mays* L.), oilseeds, and wheat (*Triticum aestivum* L.) were predominately selected at night. Forests and corn were consistently selected throughout the growing season. Wetlands and forests showed greater use rates than other habitats, with evident trade-offs as crop use increased with the timing of maturation. Activity was consistent with foraging in growing crops. Results indicate diel patterns were likely a function of short-term needs to avoid daytime anthropogenic risk, while seasonal patterns demonstrate how habitats that fill multiple functional roles — food, cover, and thermoregulation — can be optimized. Understanding selection by invasive species is an important step in understanding their potential environmental impacts in novel environments and informs their management.

Key words: wild pigs, *Sus scrofa*, habitat selection, residency time, persistence velocity, Canadian prairies

Résumé

La sélection de ressources permet de mieux comprendre l'écologie des espèces, tout particulièrement en ce qui concerne les espèces envahissantes. Depuis leur introduction au Canada, les sangliers (*Sus scrofa* Linnaeus, 1758) demeurent peu étudiés, malgré leurs impacts négatifs établis sur des systèmes indigènes et agricoles à l'échelle mondiale. Ailleurs en Amérique du Nord, les sangliers utilisent typiquement des forêts et se nourrissent de cultures. Nous avons postulé que les sangliers canadiens se comporteraient de manière semblable et, en utilisant les positions GPS de 15 spécimens, nous avons étudié leurs motifs nyctéméraux et saisonniers de sélection de ressources et de déplacement dans la région des prairies canadiennes. Durant la journée, des forêts sont sélectionnées de manière prédominante, alors que, durant la nuit, des cultures de maïs (*Zea mays* L.), d'oléagineuses et de blé (*Triticum aestivum* L.) sont sélectionnées de manière prédominante. Des forêts et des cultures de maïs sont uniformément sélectionnées tout au long de la période végétative. Les fréquences d'utilisation de milieux humides et de forêts sont plus élevées que celles d'autres habitats, et sont associées à des compromis évidents avec l'augmentation de l'utilisation des cultures au fil de leur maturation. Les motifs d'activité concordent avec une quête de nourriture dans des cultures en croissance. Les résultats indiquent que les motifs nyctéméraux sont probablement fonction du besoin à court terme d'évitement de risques d'origine humaine durant le jour, alors que les motifs saisonniers illustrent comment des habitats qui jouent plusieurs rôles fonctionnels (alimentation, couvert et thermorégulation) peuvent être optimisés. La compréhension de la sélection par des espèces envahissantes constitue un pas important pour comprendre leurs impacts environnementaux potentiels dans de nouveaux milieux et éclairer leur gestion. [Traduit par la Rédaction]

Mots-clés : sanglier, *Sus scrofa*, sélection d'habitats, temps de résidence, vitesse de persistance, prairies canadiennes

Introduction

Resource selection is a scale-dependent process, with spatial and temporal scale influencing the contribution of various environmental factors (e.g., landcover; Mayor et al. 2009) on animal landscape-use patterns. While much research focuses on the spatial scale of inference, temporal scale can be as important as resources are dynamic by nature (Orians and Wittenberger 1991; Ostfeld and Keesing 2000; Boyce et al. 2003). For example, within agriculturally dominant environments (e.g., agro-ecosystems), habitat availability can change drastically from month to month (i.e., seeding to harvest) and year to year (i.e., changes in planting strategies; Wilber et al. 2020). These dynamic landscape changes can be beneficial during the growing season by providing access to additional, high-energy forage (e.g., LaForge et al. 2017). These same changes can also increase habitat suitability of invasive species (Morelle and Lejune 2015) by providing both forage and cover (O'Brien et al. 2019; Osaki et al. 2019; Latham et al. 2020; Pasqualotto et al. 2021). As a result, it is important to understand resource selection and use at various temporal scales for invasive species within these landscapes, as this can elucidate their potential impact in novel agricultural environments.

Wild pigs (*Sus scrofa* Linnaeus, 1978) are one of the 100 most harmful invasive species worldwide (Lowe et al. 2000) and pose a considerable risk to agricultural crops (Schley and Roper 2003; Massei and Genov 2004). Agro-ecosystems and hybrid landscapes, like agro-forests, have become increasingly dominant across the globe (Eustreguil et al. 2012; Brook and van Beest 2014; Wilber et al. 2020) and wild pigs use these habitats, as they provide both cover and foraging opportunities (Massei and Genov 2004; Brook and van Beest 2014). As opportunistic omnivores, wild pigs take advantage of agricultural crops, with almost every crop type known to occur within their global range being used as food (Massei and Genov 2004). Wild pig population densities are typically greatest in areas with a heterogeneous mix of cover habitats and crops (Lewis et al. 2017). In their native range, crops make up 37%–88% of wild pig diets (Barrios-Garcia and Ballari 2012), and they typically inhabit agro-forests (Keuling et al. 2007; Keuling et al. 2008; Morelle and Lejune 2015). Similar landscapes are also abundant across North America (Brook and van Beest 2014; Wilber et al. 2020).

Since their introduction in the 1500s (Mayer and Brisbin 2008), wild pigs (i.e., domestic wild pigs who are likely a cross between Eurasian wild boar and traditional domestic pigs) have become established in 35 states in the USA (USDA 2020), showing a propensity to expand into areas with higher proportions of agriculture (Snow et al. 2017). In contrast, they have only been present in Canada since the 1980s, yet have rapidly expanded at rates greater than those in the USA (12.6 km²/year in the USA vs. 88 094 km²/year in Canada; Snow et al. 2017; Aschim and Brook 2019), particularly in the prairie provinces (i.e., Alberta, Saskatchewan, and Manitoba), due to accidental escapes and intentional releases (Brook and van Beest 2014; Michel et al. 2017). Currently, Canadian wild pig densities are unknown, but are

likely lower than what is seen in many other parts of North America given that they are newly colonizing. Yet, confirmed free-ranging invasive wild pig sightings have increased dramatically over the past three decades (from an average of two sightings/year during the 1990s to 859 sightings/year in the 2010s; R.A. Aschim and R.K. Brook, unpublished data), inducing concern over how this invasive species could be impacting prairie ecosystems. Furthermore, it is well established that wild pigs shift circadian patterns according to anthropogenic pressure, especially hunting (Singer et al. 1981; Keuling et al. 2008; Ohashi et al. 2013). Given that wild pigs can be primarily nocturnal (VerCauteren et al. 2020), they may be difficult to directly observe and attribute to damages, making it likely that documented damages have been considerably underestimated in the region to this point.

We aimed to add insight into potential wild pig impacts in Canada by quantifying resource selection and rates of use of a variety of available agricultural crops and native habitats within agro-ecosystems during the growing season. As opportunistic omnivores with a need for sufficient cover, we predicted wild pigs would (1) predominantly select for forests relative to other available cover habitats, and high-energy agricultural crops such as corn (*Zea mays* L.), wheat (*Triticum aestivum* L.), and oilseeds, as these are often the most impacted crops within other areas of this species range. They would also (2) favor native cover-providing habitats with limited human accessibility and lower visibility (i.e., forests, wetlands) during daylight hours due to hunting and other anthropogenic disturbances, while crop use would be higher at night when anthropogenic activities are typically low. Additionally, given there is high variability throughout the growing season in the quality and availability of high-energy crops, wild pigs would (3) select and use native habitats to a greater extent prior to and during seeding when annual crops were unavailable and perennial crops were in early emergence, with an increase in crop selection and use once crops had ripened and post harvest when crop residues and crops stored in fields remained available. Finally, we expected that (4) wild pig movements within crops would be reflective of foraging behaviour while movement in other habitats would be related to travel.

Materials and methods

Study area

Our study was conducted at two sites (340 km apart) located in southern Saskatchewan, Canada: a northern site situated near the town of St. Brieux (760 km²) and a southern site situated near Moose Mountain Provincial Park (1465 km²), both of which are in the Prairie Ecozone. The northern site is highly representative of agro-ecosystems in Saskatchewan, with the largest percentage of the landscape being a heterogeneous mix of crops with oilseeds and wheat, followed by small abundant pothole wetlands, and highly fragmented patches of native forests and grasslands (Table 1). While the southern site shows similarities in the heterogeneous makeup of the cropland (i.e., oilseeds and wheat are the

Table 1. Percentages of each landcover type in the northern and southern sites.

Landcover type	Northern site	Southern site
Wetlands	16.0	14.1
Water	3.4	4.5
Wetland	4.6	5.0
Too wet	<0.1	<0.1
Shrubland	8.0	4.6
Barren	4.9	3.2
Barren	2.2	0.3
Urban	2.1	1.9
Fallow	0.6	1.0
Grasslands	8.9	29.4
Pasture	8.0	19.8
Grassland	0.9	9.6
Forests	12.4	32.5
Coniferous forest	0.2	<0.1
Broadleaf forest	12.1	32.5
Mixedwood forest	0.1	<0.1
Total crops	57.8	20.7
Legumes	1.1	3.0
Oilseeds	28.6	6.7
Corn (<i>Zea mays</i>)	<0.1	0.2
Wheat (<i>Triticum aestivum</i>)	13.9	9.7
Other*	14.2	1.1

Note: Sites were delineated by a minimum convex polygon around all wild pig (*Sus scrofa*) locations and percentages are an averaged over both years. There was <4% and <8% difference between years in the northern and southern sites, respectively, between landcover types.

*Other includes barley (*Hordeum vulgare*), mustard (*Sinapis alba*), oats (*Avena sativa*), rye (*Secale cereale*), herbs, canaryseed (*Phalaris canariensis*), sunflower (*Helianthus annuus*), and hemp (*Cannabis sativa*). All of which are each <1% of the sites except barley (9.5%) and oats (4.4%) at the northern site.

most abundant crop) and has a similar amount of small pothole wetlands, grasslands and forests make up the largest percentage of the landscapes in this area (Table 1). The locations were chosen because they were known to have established populations of wild pigs, which made them the only logistically viable places to collar animals in the region at the time. The two study sites see an average of 41 cm of precipitation a year, mostly as rain during summer (June–August; Environment and Climate Change Canada 2019). Summer and winter (November–February) temperatures average 18 and –12 °C, respectively, with highs reaching 41 °C and lows at –47 °C. Once dominated by native grasslands, shallow pothole wetlands, and patches of deciduous and mixed deciduous–coniferous forest, the majority of the region now consists of annual and perennial crops (predominantly annual cereals (e.g., wheat, oats (*Avena sativa* L.), barley (*Hordeum vulgare* L.), rye (*Secale cereale* L.)), legumes (i.e., pulse crops, e.g., lentils (*Lens culinaris* Medik.), peas (*Pisum sativum* L.), soybeans (*Glycine max* (L.) Merr.), kidney beans (*Phaseolus vulgaris* L.)), and oilseeds (e.g., canola (*Brassica napus* L.), flax (*Linum usitatissimum* L.), mustard (*Sinapis alba* L.), sunflower (*Helianthus annuus* L.)) leading to a heterogeneous mix of crops and fragmented native habitats. In this region, crops are typically planted in May, mature between June and October, and are

almost fully harvested by the end of November in most years (Saskatchewan Ministry of Agriculture 2016).

GPS data collection

To examine selection and use of habitats by wild pigs during the crop growing season, we captured and collared wild pigs ($n = 26$; 22 individuals, with four collared twice) during February and March 2015 and 2016. Pigs were captured using a net gun fired from a helicopter and restrained using hobbles, blindfolds, and hog snares. Each wild pig was fitted with a GPS collar (Telonics GPS/Iridium, Arizona, USA), which was set to collect fixes at 3 h intervals and drop-off 13 months after deployment. Collars also had a VHF signal used in collar collection. Capture and handling protocols were approved by the University of Saskatchewan Animal Research Ethics Board (Animal Use Protocol No. 20150024 and Saskatchewan Ministry of Environment Permit 17FW027).

Resource selection

To examine resource selection by wild pigs, we used step-selection functions (Thurfjell et al. 2014). This analysis was chosen over more traditional analyses, such as resource selection functions, as it allows for the inclusion of a temporal component and defines availability given a species movement potential (Thurfjell et al. 2014). We first censored GPS locations occurring within the first 24 h of collaring and any locations that occurred after collars were slipped by the animal, or animal mortality was determined (per Jung et al. 2019). Next, we censored locations from collars that came off prematurely (i.e., slipped or animal mortality) and totaled less than 3 months of consecutive data. Lastly, we censored locations that were clearly incorrect (i.e., improbable locations such as those located >20 km from the study area or last location), and only data from the crop growing season (April–November) were used. We generated 10 random available locations for each used GPS location using potential step lengths and turn angles from a gamma distribution (i.e., analogous to a correlated random walk; Kareiva and Shigesada 1983). Step lengths are defined as straight-line distances between two successive GPS fixes, while turn angles are the directional change in heading between successive steps. Thus, only movement bursts with ≥ 3 consecutive locations (i.e., over a minimum of 9 h) were included in analyses to allow for the proper calculation of turn angles.

Landscape variables

Habitat variables, both crop and non-crop, were extracted for each used and available step from the Agricultural and Agri-Food Canada crop inventory maps for 2015 and 2016 (classification accuracy of $\geq 85\%$; AAFC 2015, 2016), with locations of all animals matched to the appropriate year to account for changes in crop planting. To deal with potentially confounding effects of rare cover types in the study area, and to help minimize the number of variables for analysis, landcover categories were grouped into “wetlands” (water, wetlands, too wet to seed, and shrublands),

“forest” (broadleaf, mixed, and evergreen forests), “barren” (barren, urban, and fallow lands), “grassland” (pasture and native grasslands), “legumes” (soybeans, peas, beans, and lentils), “oilseeds” (canola and flaxseed), “wheat” (winter and spring wheat), corn, and “other crops” (barley, mustard, oats, rye, herbs, canaryseed (*Phalaris canariensis* L.), sunflower, and hemp (*Cannabis sativa* L.)). The categories that made up wetlands, forest, barren, and grasslands were grouped based on their probable similarity in ecological functionality for wild pigs. We grouped legumes due to their similarity in dietary value (high protein and energy content, high starch; Navarro et al. 2019) and their low availability to pigs within the study areas (~3% of available locations). We also grouped the two most prevalent oilseeds (canola and flax) on the landscape and, as spring wheat dominated the wheat class (>99% of availability), we grouped winter wheat within this variable. Finally, “other crops” are a combination of the remaining cereals, exceedingly rare oilseeds, and herbs that made up <3% of the crops available to wild pigs in the study area (Table 1). Corn was the only variable not grouped with another crop type, since it is uniquely much taller than all other crop types, it has extremely high nutritional value, and due to the known predilection pigs have for the crop worldwide (Dardaillon 1987; Schley and Roper 2003; Herrero et al. 2006; Giménez-Anaya et al. 2008; Barrios-Garcia and Ballari 2012).

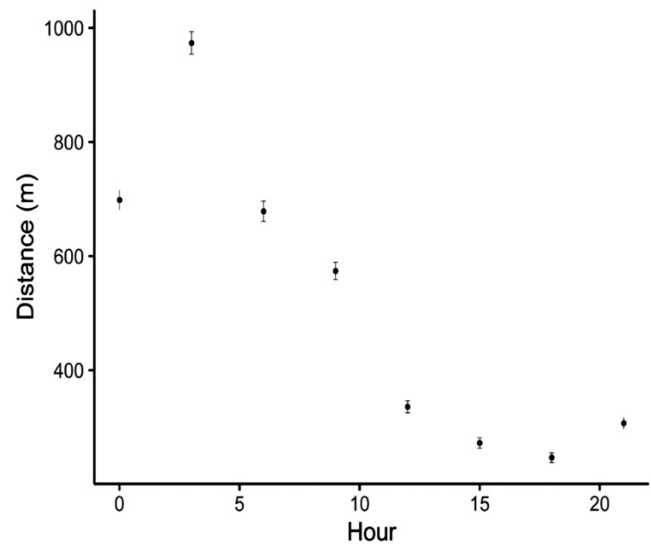
Movement

To examine potential wild pig behaviour in crops and natural habitats, we calculated residence time and persistence velocity. Daily residence time, the sum of the individual visit durations, to crop and natural habitats was calculated as a measure of persistence within each landcover type. Interpretation of residence time can be improved by distinguishing differences in movement using persistence velocity (Edelhoff et al. 2016), which was calculated for every location as the product of the estimated speed and the cosine of the turning angle (Gurarie et al. 2009). Persistence velocities that overlap zero indicate directional movement, while increasing persistence velocities with relatively small variance indicate foraging behaviour. Relating speed to the observed turning angle in the calculation of persistence velocity eliminates biases caused by varying sampling intervals such as missing locations (Edelhoff et al. 2016). Residence times were calculated using the *recurse* R package and persistence velocity was calculated using *bcpa: Behavioural change point analysis of animal movement* R package (Gurarie et al. 2009; Bracis et al. 2018).

Statistical analyses

We first examined the daily movement patterns of wild pigs using a linear mixed effects model. The model had distances travelled as a response variable, hours of the day as a fixed effect, and pig-year as a random effect to account for repeated measures for each individual wild pig in each year of data collection. As wild pigs had diel movement patterns ($\chi^2_{[7]} = 319.76$, $P < 0.001$; Fig. 1), and patterns were consistent across individuals and years, we created a period of day

Fig. 1. Mean (\pm SE) distance travelled by GPS-collared ($n = 18$) free-ranging wild pigs (*Sus scrofa*) at each 3 h interval of recorded fixes over a 24 h period in Saskatchewan, Canada, in 2015–2016.



variable corresponding to 12-h blocks with “night” including the hours of most activity (21:00–09:00) and “day” including the hours of reduced activity (10:00–20:00). We then examined resource selection using the *clogit* function in the *Survival* R package (Therneau 2015) to perform conditional logistic regression models with each strata assigned to paired *True:False* steps (1/0). Our first model included diel period as an interaction with habitat type, while our second model included each habitat type as an interaction with month. Subsequently, we examined average rates of use using linear mixed-effect models with diel period as an interaction with habitat type in the first model and then month as an interaction with habitat type for the second model. Non-landcover variables like Euclidean distance to riparian areas and urban habitats, and study site, were also considered but dropped due to their lack of explanatory power (Euclidean distance variables: $\beta < 0.001$, $P < 0.001$; study site: $\beta = -0.13$, $P = 0.92$). Residence time and persistence velocity were investigated using linear mixed-effect models using the same interaction terms as those used for resource selection. Rates of use, residence time, and persistence velocity models had pig-year as a random effect to account for repeated measures for each individual pig, and variables were square-root transformed to meet the assumption of normality. We calculated selection coefficients as the ratio of used to available locations in each habitat. Proportional use rates were calculated as the number of used locations in each habitat divided by the total number of GPS locations for each animal. All variables were averaged for both the diel and seasonal periods. Seasonal and diel selection models were assessed using Wald tests (χ^2), which are analogous to *F* tests when the number of observations is large and allow for a refined means of dealing with large degrees of freedom (Agresti 1990). All analyses were performed in R version 3.6.2 (R Core Team 2019).

Results

We collared a total of 26 pigs; however, we lost collars due to collar slippage off the animal ($n = 6$), collar failure ($n = 5$), and hunter harvest ($n = 4$). Additionally, we only used pigs with ≥ 3 months of continuous data (even with premature drop-off) in our analyses, leaving 15 study animals (5 females and 10 males; 6 at the northern site and 9 at the southern site) with a total of 18 pig-summings of data (i.e., 1 pig-summer = 1 pig collared for 1 summer). Collars had a spatial accuracy of 6 m based on field tests (i.e., ad hoc tests from deployed collars that had dropped off or mortality had occurred; [Villemiquet et al. 2008](#)) and an average fix success rate of 90.2% (i.e., successful GPS fixes divided by GPS fix attempts; [Jung et al. 2018](#)).

Diel selection and rates of use

Wild pig selection of crops and natural habitats during the growing season varied by diel period (Supplementary Table S1) with crops being selected for more often during the night compared with the day ([Fig. 2a](#); Supplementary Table S1). Of all the habitat variables, only corn and forests were selected for during day and night; however, selection was strongest at night for corn and strongest during the day for forests (Table S1; [Fig. 2a](#)). Oilseed and wheat were selected for at night and avoided during the day ([Fig. 2a](#); Supplementary Table S1). Wetlands were avoided at night and mostly avoided during the day, while legumes were avoided during the day and mostly selected for at night ([Fig. 2a](#); Supplementary Table S1). Barren areas, grasslands, and other crops were always avoided by wild pigs but less so during the night ([Fig. 2a](#); Supplementary Table S1). In contrast to selection, wild pigs had similar diel proportional rates of use across habitat types although individual habitats were used at different rates ([Fig. 2b](#); Supplementary Table S2). Most habitats had relatively low rates of use ($< 8.1\%$), although wetlands and forests were used $14.5\% \pm 2.0\%$ (mean \pm SE) and $55.2\% \pm 4.0\%$ of the time, respectively ([Fig. 2b](#)).

Seasonal selection and rates of use

Wild pig selection of crops and natural habitats varied by month (Supplementary Table S3). Corn was the only crop selected for consistently over the course of the entire growing season, with selection occurring in April, before the planting season, and then from August–November as the crop continued to mature ([Fig. 3a](#); Supplementary Table S3). Legumes, oilseeds, and other crops, along with barren areas and grasslands were always avoided ([Fig. 3a](#); Supplementary Table S3). Wheat and wetlands were generally avoided but were increasingly selected for after plant maturation ([Fig. 3a](#); Supplementary Table S3). Only forest was consistently selected for each month ([Fig. 3a](#); Supplementary Table S3).

Wild pig proportional rates of use also varied by month for each habitat type ([Fig. 3b](#); Supplementary Table S2). Corn, wheat, legumes, and other crops had low use rates overall. However, rates of use increased 23.5-, 2.3-, 4.3-, and 5.7-fold as plants matured into July, respectively, with those rates declining again as harvest proceeded from August through the fall period ([Fig. 3b](#)). Grassland use rates were also relatively

low. However, grassland use increased 3.2-fold from April–July before declining 1.8-fold and then remaining consistent throughout the remainder of the growing period ([Fig. 3b](#)). Oilseed, wetlands, and barren areas had consistent rates of use throughout the growing period ($10.3\% \pm 1.0\%$, $15.0\% \pm 1.3\%$, and $1.8\% \pm 0.3\%$ respectively; [Fig. 3b](#)), while forests had the highest rates of use and were used to a greater extent pre- and during planting, early crop maturation, and post harvest, with the lowest use during July and August ([Fig. 3b](#)).

Movement

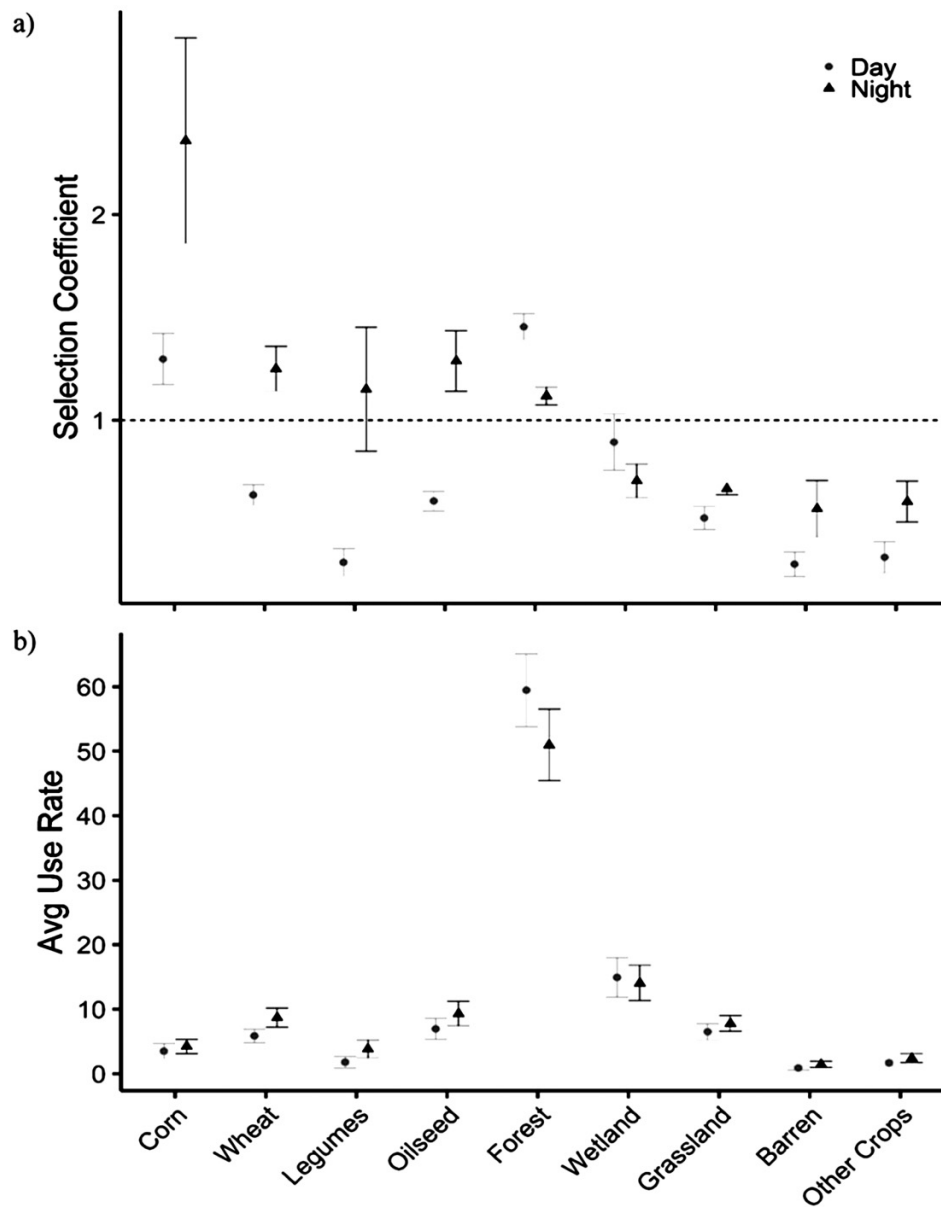
Overall, diel residency was similar between day and night within a habitat type ([Fig. 4a](#); Supplementary Table S4). Residency was highest in corn (11.7 ± 0.9 h) followed by forest, wetland, oilseeds, grasslands, wheat, legumes, barren lands, and other crops ([Fig. 4a](#); Supplementary Table S4). In contrast, persistence velocity varied by diel period for each habitat type (Supplementary Table S4) and was higher at night within forest, wetland, and barren habitats ([Fig. 4b](#)).

Wild pig residency varied by month for each habitat type (Supplementary Table S4) with residency being greater than the 3 h fix interval (i.e., in a particular habitat for longer than 3 h) for corn, forests, wetlands, oilseed, and wheat ([Fig. 5a](#)). Corn residency occurred in April and May, before the planting season, and then from August, peaked in September (20.1 ± 1.3 h), and remained above 6 h per day in October and November ([Fig. 5a](#)). Residency time in forests and wetlands remained fairly consistent (between 8 and 12 h; [Fig. 5a](#)). Additionally, residency time in oilseeds and wheat increased from June through September ([Fig. 5a](#)). Persistence velocities also differed by month and habitat type (Supplementary Table S4), with positive persistence velocities with low variation occurring consistently in corn, legumes, oilseeds, and wheat ([Fig. 5b](#)). Persistence velocities overlapping zero in barren and other crops indicated largely directional travel ([Fig. 5b](#)).

Discussion

Our results provide strong evidence of differences in diel and seasonal selection throughout the growing period by wild pigs in agro-ecosystems. Forests and corn were selected during both day and night, but forest selection was stronger during the day, while corn along with oilseeds and wheat had stronger selection during the night (corroborating predictions 1 and 2). Corn and forests were also consistently selected for throughout the growing season. Although rates of use did not differ by diel period, they did vary seasonally, with wetlands and forests showing higher rates of use over other habitat types. Additionally, the trade-off between crops and natural habitats persisted with all crop types showing a peak in use between July and September when most crops are mature and most natural habitats (e.g., forests) being used at other times during the growing season (corroborating prediction 3). Movement behaviour indicated activity consistent with foraging in these months (corroborating prediction 4). Our results demonstrate that (i) wild pigs make important trade-offs between hiding cover and agricultural food sources that change as crops mature to optimize feeding time, (ii) crops themselves provide hiding and thermal cover

Fig. 2. (a) Mean (\pm SE) selection coefficients and (b) mean (\pm SE) rates of use (%) for corn (*Zea mays*), wheat (*Triticum aestivum*), legumes, oilseed, forest, wetland, grassland, barren areas, and other crops during the day and at night by GPS-collared ($n = 18$) free-ranging wild pigs (*Sus scrofa*) in Saskatchewan, Canada, in 2015–2016 (note the varying y axes).



during mid-summer, and (iii) crops are at greatest risk from wild pigs at night and during peak crop maturation when forage value is highest.

Differences in diel selection by wild pigs in agro-forests can likely be attributed to anthropogenic activities, especially hunting (Ohashi et al. 2013; VerCauteren et al. 2020). Throughout their global extent, wild pig activity can vary; however, wild pigs are predominantly nocturnal when diurnal anthropogenic activities cause disturbances (Ohashi et al. 2013; Johann et al. 2020; VerCauteren et al. 2020). For example, hunting pressure has led to increased nocturnal behaviour of wild pigs in some areas (Keuling et al. 2008; Ohashi et al. 2013) and an increased use of the forest (Tolon et al. 2009; Merli et al. 2017). Similar trends can be seen

in other species such as brown bears (*Ursus arctos* Linnaeus, 1758), which, despite their naturally diurnal nature, shift to nocturnal behaviour (i.e., 75% of activity occurring at night) to reduce human conflict and increase survival (Lamb et al. 2020). Hunting pressure for wild pigs is widespread in our study area given the year-round open season during daylight hours with no harvest limits (e.g., 4 of the 22 collared animals were shot by hunters during our study). Agricultural activity (e.g., seeding, herbicide application, cutting, harvesting, and tilling) is another form of disturbance that is widespread throughout our study area, peaking during spring seeding, summer herbicide application, and fall harvest and farmers have been known to kill wild pigs observed during the day while conducting farm operations. The intensity of

Fig. 3. (a) Mean (\pm SE) selection coefficients and (b) mean (\pm SE) rates of use (%) for corn (*Zea mays*), wheat (*Triticum aestivum*), legume, oilseed, forest, wetland, grassland, barren areas, and other crops from April to November 2015–2016 by GPS-collared ($n = 18$) free-ranging wild pigs (*Sus scrofa*) in Saskatchewan, Canada (note the varying y axes).

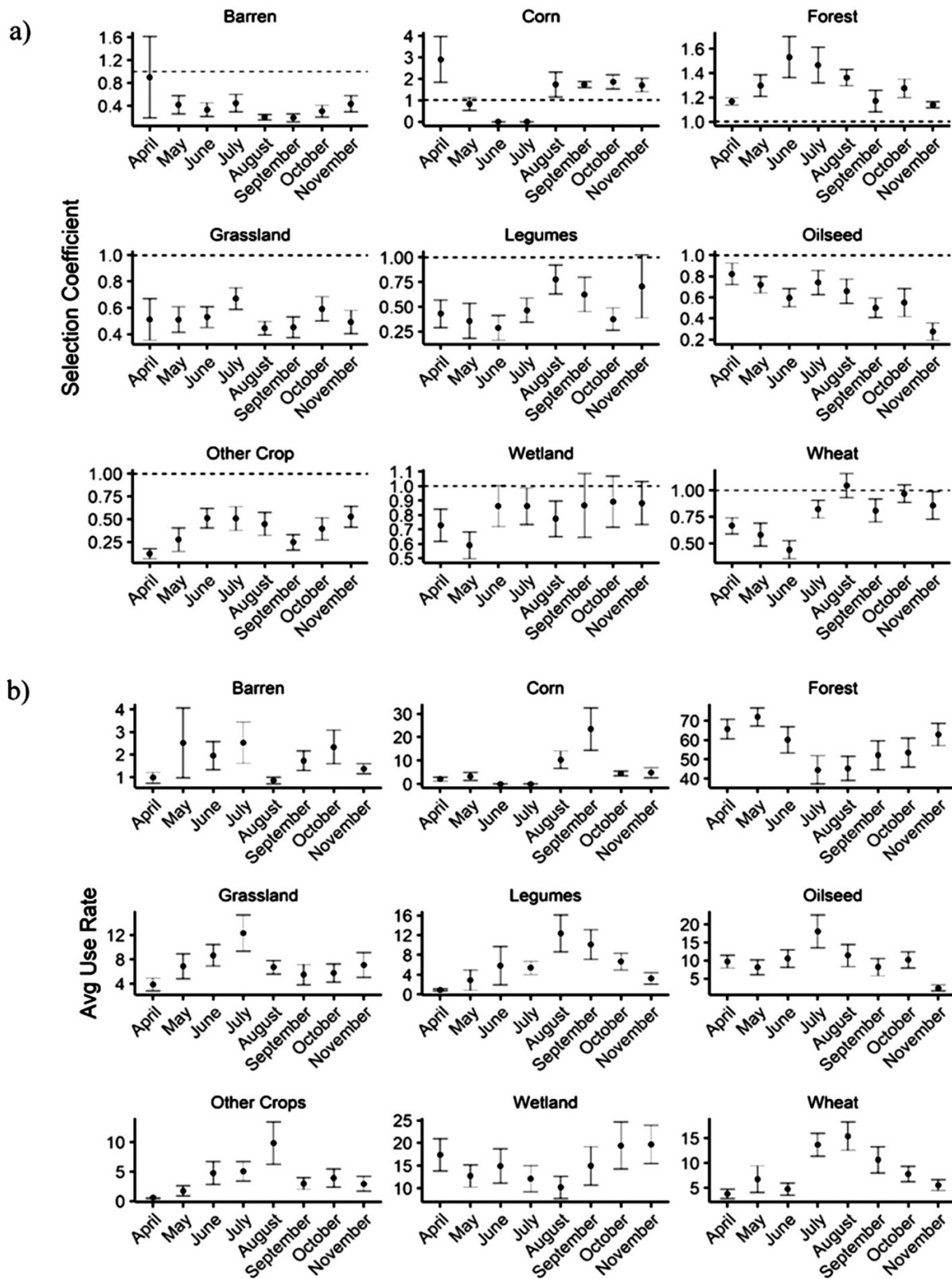
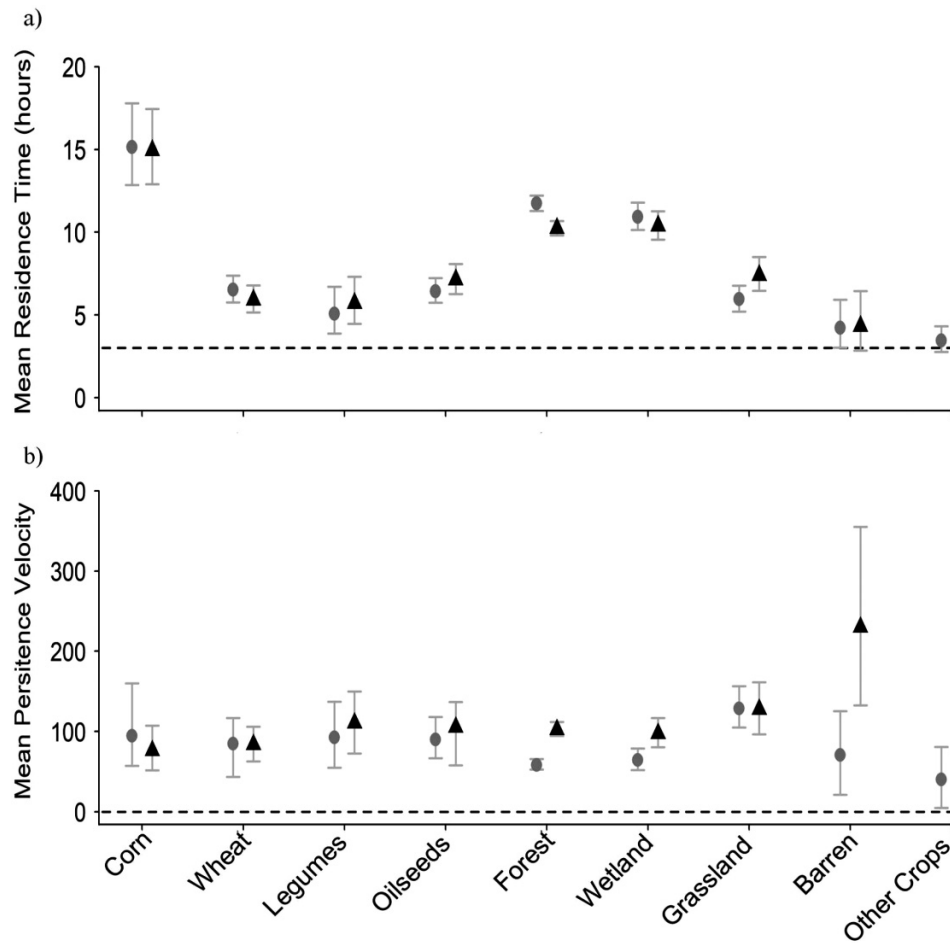


Fig. 4. (a) Mean (\pm SE) residence time and (b) mean (\pm SE) daily persistence velocity for corn (*Zea mays*), wheat (*Triticum aestivum*), legumes, oilseed, forest, wetland, grassland, barren areas, and other crops during the day and at night by GPS-collared ($n = 18$) free-ranging wild pigs (*Sus scrofa*) in Saskatchewan, Canada, in 2015–2016.

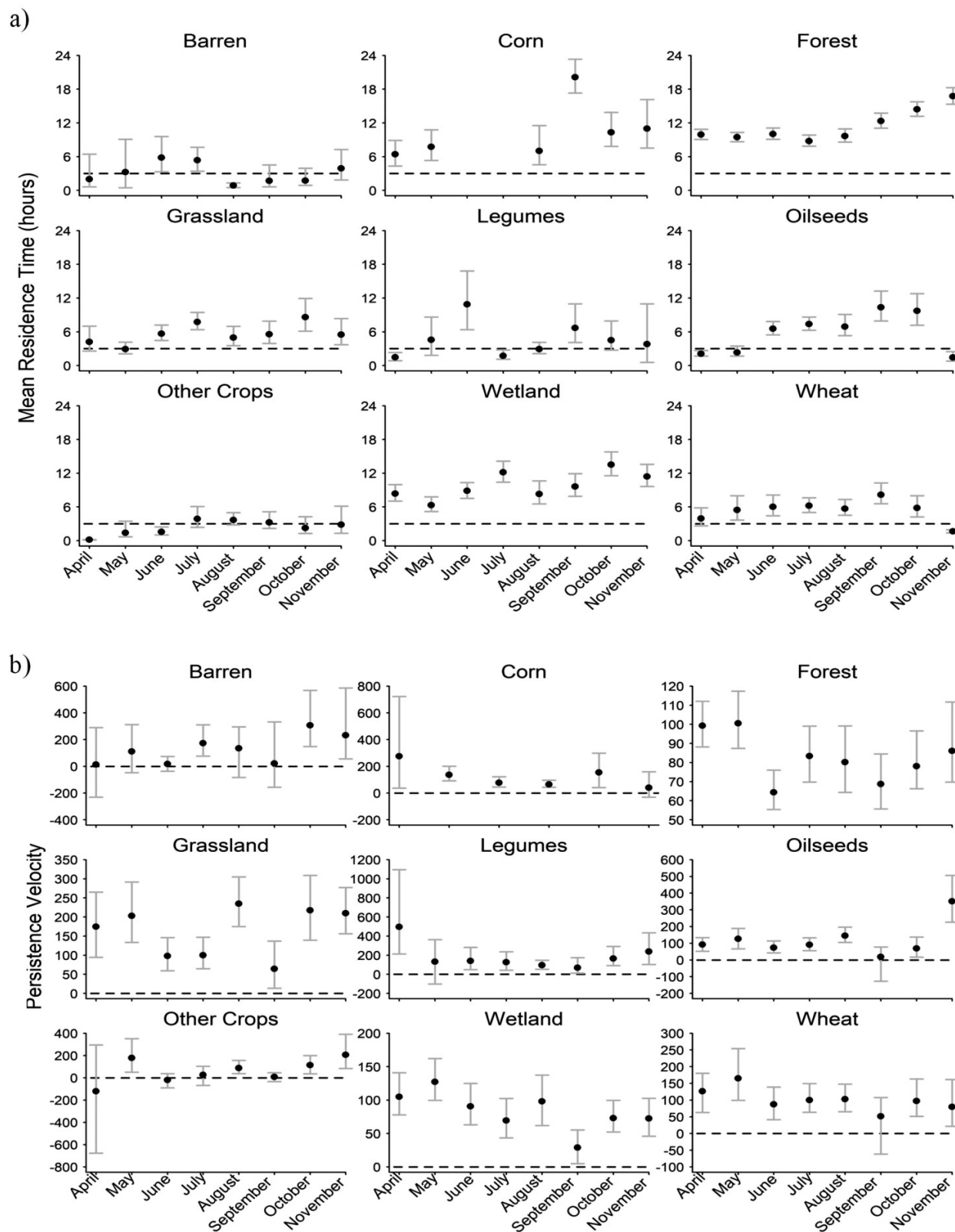


anthropogenic activity during the day likely results in wild pigs using crops more at night to reduce risks that would otherwise be associated with crop fields. Indeed, open areas were readily avoided by pigs in our study with behaviour consistent with rapid directional movement. However, it is important to note that wild pigs also need thermoregulatory cover during hot summer days, and the use of forest cover and taller crops can provide suitable habitat to reduce solar exposure. As a result, forest selection during the day not only mitigates potential human conflicts, but also provides shade that is important thermoregulatory relief during periods of heat and intense sunlight (as wild pigs are poor thermoregulators due to their lack of sweat glands; VerCauteren et al. 2020) and a variety of food sources (hard mast, bulbs, roots, etc.; Ballari and Barrios-García 2014). These attributes are likely why wild pigs show not only a strong selection for forest, but also six times the rate of use compared to crop lands. It is notable, however, that corn also provides an optimal mix of food and thermoregulatory capacity (i.e., cover; as seen in Santos et al. 2004; Paolini et al. 2018), given the leaves face upward to collect sunlight and reduce exposure to UV light. In comparison, other taller crops like oilseeds and wheat are viable high-energy food sources that may lack the

canopy cover to provide sufficient thermoregulatory relief. Thus, our results highlight how wild pigs can optimize their use of agro-forested landscapes. They are able to avoid anthropogenic pressures and use high-energy and cover-providing crops to their advantage, as crops perhaps subsidize colonizing pigs in northern agro-ecosystems that may be poor in mast resources.

Previous research has demonstrated that wild pigs are adept at taking advantage of seasonally available crops (Giménez-Ayana et al. 2008; Morelle and Lejune 2015; Wilber et al. 2020), with the availability of crops during the growing season nearly doubling wild pig habitat suitability (Morelle and Lejune 2015). Additionally, crop availability can change wild pig home range distribution, with home ranges that were originally centered between forests and agricultural crops changing over completely to agriculture when crops are mature (Keuling et al. 2007). At the seasonal scale, crop selection was dampened relative to diel selection patterns (similar to Morelle et al. 2016) for everything except corn which is unsurprising considering corn is the crop most damaged by wild pigs worldwide due to its high nutritional value (Schley and Roper 2003). Indeed, corn was the only crop to show selection prior to planting (i.e., April), despite the fact plants are

Fig. 5. (a) Mean (\pm SE) residence time and (b) mean (\pm SE) daily persistence velocity for corn (*Zea mays*), wheat (*Triticum aestivum*), legumes, oilseed, forest, wetland, grassland, barren areas, and other crops from April to November 2015–2016 by GPS-collared ($n = 18$) free-ranging wild pigs (*Sus scrofa*) in Saskatchewan, Canada (note the varying y axes).



no longer standing after winter. However, it is possible residual amounts of the crop would be available from silage harvest or livestock grazing after the snow had thawed, which wild pigs seemingly took advantage of. In Saskatchewan, substantial amounts of starch within corn kernels do not occur until August (Bell 2017), which corresponds to the first month of selection for this crop after seeding. Corn was the only crop in our study that showed consistent positive selection for the entire growing season post-planting, and while its use does decline after September, as with all other crops given the beginning of harvest, corn is still selected for from October through November, which could be due to a combination of fields left standing for livestock grazing and residual crop left behind in harvested fields; all these points highlight its nutritional value to wild pigs.

While wild pig behaviour in crops such as wheat was consistent with foraging activity, given dampened selection for other crop types, cover may have been a stronger driver of seasonal habitat selection. For example, forests cover was strongly selected and used during the entire study period. However, forest is not the only cover-providing habitat; corn and wheat are both tall enough to provide cover, and both had increased selection more than 2 months post planting, further highlighting the importance of cover. Although other tall crops, like oilseeds, are used as both food and cover elsewhere (Keuling et al. 2007), they were consistently avoided seasonally, a trend which may be attributed to the inability of this habitat to fulfill multiple ecological roles to the degree corn and wheat do. However, oilseeds and wheat also show markedly greater use than corn seasonally and daily, and behaviour in these crops was consistent with foraging, indicating that their combination of high-energy food and cover is important but is likely a function of their increased availability on the landscape relative to corn. Therefore, the contrasting selection results highlight the overall importance of the food–cover–thermoregulatory triad, especially with the inclusion of forest, the most used and selected for habitat seasonally and daily.

Finally, all crops, especially shorter crops only showed increased rates of use as they ripened (sensu Wilber et al. 2020), while wetlands, which are typically very important to wild pig thermoregulation (i.e., by providing access to water and mud wallows; Paolini et al. 2018), showed high rates of use but minimal selection. This is likely because the study area falls within the Prairie Pothole region of North America and wetlands, while typically small, are widespread and abundant throughout both study areas. As such, our findings indicate that habitats providing both hiding/thermoregulation cover and rich food sources (e.g., forest, corn, and wheat) are those most important to wild pigs at a seasonal scale within Canadian agro-ecosystems during the growing season. However, within our study area, mast-producing trees are rare, so food sources would likely consist of bulbs, fruits, forbs, mushrooms, and seeds in forests. The lack of the most consumed primary natural food sources of wild pigs during the fall likely adds an increased dietary burden on other sources (such as agricultural crops).

We acknowledge certain limitations associated with our work. First, we acknowledge our limited sample size. Given

that wild pigs are novel in Canada, finding study animals was a significant challenge when they exist at low densities. Furthermore, sample sizes become even more limited for wild pigs as many individuals will slip collars due to their morphology and some will be shot by hunters. Despite this, ecologically based inferences have been made using similar sample sizes for studies on wild pigs in the USA (Paolini et al. 2018, 2019; Gray et al. 2020; Sanders et al. 2020; Yang et al. 2021), making us able to at least compare our results to other locales. Finally, recent work suggests that sample sizes of <30 animals are frequently adequate in resource selection analyses (Street et al. 2021). We also recognize that a 3 h fix rate may be the course for understanding residence time and persistence; however, all our metrics exceeded the fix rate (particularly for corn) indicating that wild pigs spend a large amount of time within landcover types and that our cursory examination of wild pig activity may be sufficient. Further research is needed to adequately understand wild pig impact on the landscape and how best to tailor management strategies. For example, GPS collars with cameras that collect photos and (or) video, or three-dimensional accelerometers, will provide more fine-scale detail in understanding what exactly wild pigs are doing within the landscapes they inhabit.

Future research should also examine wild pig responses to hunting and the potential role of predators in wild pig control as wild pigs expand into the boreal forest, as well as the impact wild pigs may have on co-occurring native fauna. Our results raise additional concerns regarding species interactions within agro-ecosystems as wild pigs are not the only species to take advantage of available cropland, native elk (*Cervus canadensis* Erxleben, 1777), moose (*Alces alces* (Linnaeus, 1758)), white-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780)), and mule deer (*Odocoileus hemionus* (Rafinesque, 1817)) often use these areas (Sorensen et al. 2015; LaForge et al. 2017) and likely interact with wild pigs (O'Brien et al. 2019; Brook and Clarke 2020), the effect of which is unknown. Additionally, while wheat and oilseeds are the most abundant crops on the landscape, it is unlikely that their overall availability will change substantially; however, corn production is expected to increase throughout our study region and this increased availability is likely to have a profound effect on wild pig use and selection, providing a positive functional response (sensu Mysterud and Ims 1998) at current pig densities. These changes may also contribute to a significant agricultural population subsidy, with greater wild pig densities leading to stronger selection tendencies (van Beest et al. 2016), which will intensify crop predation and native fauna interactions as pig densities continue to increase exponentially across the prairie provinces of Alberta, Saskatchewan, Manitoba, and potentially beyond.

Resource selection is commonly examined when trying to understand the ecology of a wide range of native fauna but is used less frequently with invasive species (DeGrandchamp et al. 2008; Wang and Li 2009; Walters et al. 2016; Wysong et al. 2020). Additionally, studies tend to focus on a single temporal scale, although the hierarchical nature of selection lends itself to studies that use a multi-scale approach to more broadly understand selection tendencies and interpret behaviour (Johnson 1980; Mayor et al. 2009). For example,

moose make important trade-offs between quality foraging habitat during the day and hiding cover at night (Bjørneraas et al. 2011) while mule deer selected for areas of higher forage quality prior to parturition and areas that reduce the risk of predation of neonates after parturition (Long et al. 2009). This temporal aspect is particularly important in highly seasonal northern agro-ecosystems where there are dramatic changes in crop quality through the growing season. Here, we show crop vulnerability to an invasive species is dependent on crop height and its ability to facilitate the evasion of anthropogenic pressures. Our findings thus provide an important step into further elucidation of wild pig ecology and its impact in novel Canadian agro-ecosystems.

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Data availability

Movement data is provided in MoveBank.

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RKB and RP collected data; CJK performed analyses and wrote the first manuscript draft; MRB helped with analyses and writing of the first draft; RKB and CJK helped with study

design; RSM and KCV contributed conceptually; all authors contributed to revisions.

Competing interests

The authors declare that there are no competing interests.

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Supplementary material

Supplementary tables are available with the article at <https://doi.org/10.1139/cjz-2021-0116>.

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