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Discerning the Environmental Drivers of Annual Migrations in an Endangered Amphibian

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The prevalence of studies that discern the drivers of animal migrations is increasing exponentially, in line with raised concerns over climate-driven shifts in phenological patterns. Amphibians that breed in ephemeral wetlands are particularly vulnerable owing to the stochastic nature of their breeding habitat and high survival and reproductive costs associated with untimely migrations. Knowledge of the effects of climatic cues on the timing of amphibian migration and breeding phenologies is required to understand the potential consequences of climate change and to inform conservation plans for at-risk species. Here we use six years of count data from Eglin Air Force Base, Florida, U.S., collected between 2010 and 2016, to model the phenology of migrations of *Ambystoma bishopi*. Models were fit with a negative binomial error distribution, with daily values of temperature and precipitation as covariates. Models were compared in an AIC framework. We found that salamander movement was strongly tied to environmental cues. A proclivity to move over a medial range of temperatures and precipitation resulted in a 'Goldilocks' set of conditions that facilitate migration. We also discovered a role for endogenous drivers of movement, with day of year predicting above-ground activity regardless of environmental conditions. These results contribute to our basic knowledge of the behavior of *A. bishopi* and provide managers with useful metrics to maximize the efficacy of conservation actions. More broadly, the methods employed within have utility to amphibian researchers to help predict the effects of climate change and tailor management strategies accordingly.

ENVIRONMENTAL factors that determine phenological patterns in nature have received increasing attention, partly driven by increasing concerns of climate change and concomitant phenological mismatches (Roy and Sparks, 2000; Menzel et al., 2006; Kelly et al., 2016; Green, 2017). Climate-driven shifts in the timing of key life-history events are predicted to have consequences at the species and community level (Edwards and Richardson, 2004; Thackeray et al., 2010; Valtonen et al., 2011). For example, asynchronous shifts in phenologies across taxa may disrupt plant–pollinator mutualisms (Hegland et al., 2009), decouple latitudinal migrations from resource availability (Both and Visser, 2001; Post and Forchhammer, 2008), and lead to mismatches between peak food availability and reproduction (Visser et al., 1998, 2006; Plard et al., 2014). Developing a better understanding of the environmental cues that underlie phenologies is fundamental for predicting the responses of species to a changing environment, and thus development of steps toward mitigating the effects of climate change.

Many amphibians in temperate regions undertake annual migrations from terrestrial upland habitat to aquatic breeding habitats (Semlitsch, 2008). In the southeastern United States (U.S.), many amphibians rely on ephemeral (i.e., temporary) wetlands for reproduction and larval development (Russell et al., 2002; Gibbons et al., 2006). Adults must use environmental cues to time movements to coincide with seasonal precipitation events that fill wetlands in order to allow maximum development time for larvae before water levels recede. In addition, adults must time above-ground movements with environmental conditions that mitigate the risk of desiccation. Accordingly, amphibian migrations to and from breeding wetlands have been linked to climatic variables such as daily rainfall and temperature (Jakob et al., 2003; Cook et al., 2006; Todd and Winne, 2006; Timm et al., 2007; Canavero et al., 2008).

Climate projections for the southeastern U.S. suggest warmer mean temperatures, shifts in the frequency and timing of rainfall events, and longer periods of drought (Strzepek et al., 2010; Bucklin et al., 2013; Ingram et al., 2013; Chandler et al., 2016). Clearly such environmental change is pertinent to amphibian ecology and future management of threatened and endangered species (Beebee, 1995; Walls et al., 2013; Chandler et al., 2016; Green, 2017). To direct conservation efforts, additional long-term studies of the environmental cues underlying amphibian movements are needed, especially given the observed declines of many species (Stuart et al., 2004; Alford, 2010).

Here, we evaluate linkages between environmental variables and the timing of breeding movements between upland habitat and ephemeral wetlands of Reticulated Flatwoods Salamanders (*Ambystoma bishopi*; hereafter flatwoods salamanders). Flatwoods salamanders are considered federally endangered under the U.S. Endangered Species Act (USFWS, 2009) and vulnerable by the IUCN (Palis and Hammerson, 2008). Loss and alteration of preferred habitat are often implicated in the decline of populations (Means et al., 1996; USFWS, 1999, 2009). Climate change may also have ramifications for the persistence of flatwoods salamander populations if it leads to shifts in the timing of above-ground movements that underlie breeding phenologies or shortened hydroperiods of breeding wetlands. Understanding the potential consequences of climate change requires knowledge of the effects of climatic cues on phenological patterns.

Flatwoods salamanders inhabit longleaf pine *(Pinus palustris)* flatwoods and savannas in the southeastern Coastal Plain in the U.S. Adults are fossorial and occupy mesic upland habitats, but migrate to ephemeral wetlands with

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well-developed herbaceous ground cover and relatively open canopy to breed (Palis, 1997; Gorman et al., 2009, 2014). Unlike most other North American amphibians, flatwoods salamanders lay their eggs in dry wetland basins before they fill, allowing embryos to develop so that eggs can hatch immediately when wetlands are inundated a few weeks, or months, after laying (Anderson and Williamson, 1976; Palis, 1997; Gorman et al., 2014). Although anecdotally flatwoods salamanders migrate following the first cool rains of fall, direct quantification of the drivers of movement are lacking. Previous studies of flatwoods salamander movements have been purely descriptive (Erwin et al., 2016), conducted over relatively short time periods (Palis, 1997), or have only considered crude measures of climatic variables (e.g., seasonal rainfall; Palis et al., 2006). Empirical assessment of the cues driving flatwoods salamander migrations is needed in order to inform conservation plans for this imperiled species. Being able to predict amphibian movement has additional utility, for scheduling research activities, protection efforts at road-crossings, or potentially disruptive activities in the uplands surrounding breeding sites.

MATERIALS AND METHODS

Study site.—Our study was conducted on Eglin Air Force Base (hereafter Eglin), Okaloosa County, Florida, U.S. from 2010 to 2016. Eglin is a large military installation (188,459 ha), primarily consisting of actively managed Longleaf Pine dominated sandhills (approximately 145,000 ha) interspersed with treeless open test ranges, pine plantations, and mesic flatwoods. The landscape is punctuated by ephemeral wetlands consisting of shallow depressions of low topography, which fill in the fall or early winter and typically remain inundated throughout the spring (Chandler et al., 2016). We focused on two wetlands, approximately 500 m apart, which have been monitored intensively since 2009 and that are known to be occupied by flatwoods salamanders. Both wetlands are approximately 0.4 ha and are characterized by open overstories dominated by Longleaf Pine, Slash Pine (*P. elliottii*), and Pond Cypress (*Taxodium ascendens*), and midstories dominated by Myrtle Dahoon (*Ilex cassine var. myrtifolia*), Chapman's St. John's-wort (*Hypericum chapmanii*), and Swamp Titi (*Cyrilla racemiflora*). Wetland ecotones and portions of basins used for breeding are dominated by grasses, including *Aristida stricta* and bluestems (*Andropogon* spp.) and forbs, including Flattened Pipewort *(Eriocaulon compressum*).

Sampling design.—To monitor the movements of flatwood salamanders, both wetlands were completely encircled with drift fences and funnel traps (see Erwin et al., 2016 for details). The drift fences were constructed from 60 cm tall metal flashing buried in the sediment approximately 15–20 cm. Funnel traps measuring 85 cm x 20 cm were placed flush with the fence and ground at approximately 10 m intervals on both sides of the fence. We began drift fence operations on or before the first major rains were forecast in fall, typically late October or early November. Once we initiated drift fence operations, we checked traps multiple times per night through March if water levels receded and there were no larvae present, or May if the wetlands continued to hold water. In some years, we ceased operations for a week in late December and some weekends due to staffing shortages. Our data comprise 892 sampling nights spanning six breeding seasons from fall 2010 to spring 2016; specific dates of active sampling are reported in Supplemental Table A (see Data Accessibility). Upon capture, we recorded the date and time of capture, and uniquely marked each individual using passive integrated transponder (PIT) tags or visual implant elastomer (VIE). Animals were sexed if possible, and released immediately after marking on the opposite side of the fence from their capture location. Between sampling events, we closed traps and removed sections of the fence panels to allow free movement of animals to and from wetlands.

Environmental variables.—Rain gauges were not installed for all but the last two years of our study, and so we used PRISM data at the highest resolution (800 m) in lieu of more precise information. For the two years in which rain gauge data were available, precipitation was highly correlated between the two datasets. We collected daily precipitation and temperature data from the PRISM Climate Group for the years 2010 to 2016 (Oregon State University, http://prism.oregonstate.edu, created 1 May 2017). The PRISM data set is derived from climatologically aided interpolation that averages across multiple stations and adjusts values for the grid reference of interest using output from a digital elevation model.

Statistical analyses.—To elucidate patterns in the timing of above-ground movements and the environmental factors that trigger migration, we fitted several competing generalized linear models (GLMs). Daily counts were modeled with daily precipitation, minimum daily temperature, and day of year as predictors. We considered both linear and quadratic functions of all predictors to retain flexibility in the relationships with the response. Year was included as a fixed effect, and an interaction between temperature and rainfall was explored. A high proportion of individuals of unknown sex prevented sex from being included as a random effect. Emerging metamorphs were excluded from the analysis. We evaluated collinearity between predictor variables using Spearman's rank correlation and omitted one of a pair of variables when $|r| < 0.5$ to minimize challenges associated with multi-collinearity (Dormann et al., 2013). We used Durbin-Watson statistics on model residuals to check for serial autocorrelation.

Preliminary analyses revealed that the negative-binomial distribution (NB) outperformed Poisson, zero-inflated Poisson, and Poisson-log normal error distributions. The NB parameterization can account for overdispersion commonly seen in biological data (Bliss and Fisher, 1953; Ver Hoef and Boveng, 2007; Lindén and Mäntyniemi, 2011). Failure to account for overdispersion in count data could lead to erroneous conclusions regarding the effect of covariates and ultimately lead to misguided conservation actions (Terceiro, 2003; Ver Hoef and Boveng, 2007). All results reported assume a NB error distribution, and all models were fitted in R using the statistical package 'MASS' using the glm.nb function (R Core Team, 2015).

All possible combination of variables were fit to the data, and models were compared in an AIC framework. Model selection was based on AIC weights and minimizing uninformative parameters (Arnold, 2010). Cross correlation analysis was implemented to reveal any lag effects between predictor and response, and collinearity between predictors was tested through inspection of variance inflation factors. For individuals of known sex, comparison between dates of movement for males and females were made with Wilcoxon rank-sum tests.

Table 1. Model comparison of the top five performing models based on AIC values and Akaike weights (w_i). The null model is included for reference. All models presented assume a negative binomial error distribution. Variables included are daily precipitation (ppt), minimum daily temperature (t_{min}), day of year, and year. Quadratic terms include all lower order polynomials (e.g., $Day^2 = Day + Day^2$).

Model	AIC	ΔAIC	w_i
$\sim ppt^2 + t_{min}^2 + Day + Year$	1634.3	0.0	0.33
$\sim ppt^2 + t_{min}^2 + Day + Year + (ppt * t_{min})$	1634.9	0.5	0.25
$\sim ppt^2 + t_{min}^2 + Day^2 + Year$	1635.5	1.2	0.18
$\sim ppt^2 + t_{min}^2 + Day^2 + Year + (ppt * t_{min})$	1636.2	1.9	0.12
$\sim ppt^2 + t_{min} + Day + Year + (ppt * t_{min})$	1638.0	3.7	0.05
Null	1780.0	145.7	0.00

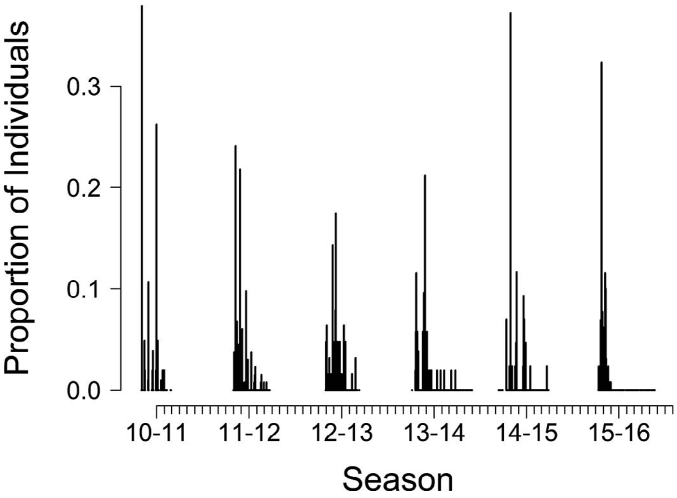

Fig. 1. Daily counts of individuals as a proportion of the total number of individuals available for capture for each year. Major tick marks are set at January 1, and minor tick marks are months.

RESULTS

Over the duration of the study, flatwoods salamanders were detected on 179 separate sampling nights (179/892 = 20%) yielding 1025 total captures (Year 1 = 164, 2 = 231, 3 = 128, 4 = 118, 5 = 79, 6 = 305). During the study period, minimum daily temperatures averaged 9.1°C (range: –8–24.4°C), and precipitation averaged 5.5 mm (range: 0–139.9 mm). Of the nights that salamanders were captured, minimum temperatures averaged 11.7°C (range: –1.5–22.5°C), and precipitation averaged 7.9 mm (range: 0–92.7 mm). Year-specific demographic and environmental information is summarized in Supplemental Table B (see Data Accessibility).

The top five performing models and corresponding AIC values are presented in Table 1. The top four models all have sufficient AIC weights to warrant consideration; however, the top model reduces the number of uninformative parameters and represents the most parsimonious description of the data. The top model includes quadratic terms for precipitation and temperature. Initially, we considered mean, minimum, and maximum daily temperatures, but subsequently excluded mean and maximum temperatures owing to the high degree of correlation between all three variables.

Both temperature and precipitation exhibited nonlinear relationships with salamander movement. The steepness of the contours, across both the precipitation and temperature axes, suggests distinct thresholds in environmental conditions that trigger salamander movement (Supplemental Figure A; see Data Accessibility). Intermediate values of temperature and precipitation were correlated with the highest movements, with a monotypic peak in movement occurring at 14°C and 43 mm of rainfall. The relationships between climatic variables and movement were qualitatively similar across all model parameterizations. There was further evidence for a lagged effect of minimum daily temperatures on salamander movement; overland migrations were more strongly correlated with temperature in previous time steps (results not shown). In contrast, the effect of precipitation on salamander movement showed no evidence of a time lag. The second best performing model also contained an interaction between temperature and precipitation. At low temperatures, increased precipitation was predicted to have a larger positive effect on salamander movement compared with an equivalent increase at high temperatures.

Irrespective of environmental conditions, day of year influenced salamander activity; movements were concentrated around October, representing peak arrival dates, with above-ground movement declining as the season progressed. Year was retained in the top model parameterization, indicative of annual variation in movement patterns (Fig. 1). In three of the six years, over 20% of the breeding population migrated to wetlands on a single night.

Although we found no overall difference between the timing of movements of males and females (Wilcoxon rank-sum test, $P = 0.84$), there were noticeable differences within years (Fig. 2). In fall of 2011 and 2015, males arrived earlier than females, whilst in fall of 2013, females arrived earlier than males (Fig. 2). In all other breeding seasons, there was no difference in arrival times between the sexes.

Predicted frequencies from the top-performing model provided a good fit to the observed data (Chi-Sq = 13, $P = 0.2$). Predictive accuracy is high for peak movement nights (>40 individuals) and daily counts below 15 individuals; however, the model tends to over-predict the frequency of nights with 25–35 individuals and under-predict nights with no captures. Comparison of the observed frequency distribution of arrivals with those expected under the top model are reported in Supplemental Figure B (see Data Accessibility).

Serial autocorrelation is a common concern in studies of count data, particularly when movement occurs in clusters; however, we found no evidence of correlation between the model residuals and thus serial autocorrelation does not appear to be an issue in our data (Durbin-Watson statistic = 2.3, $P = 0.9$).

DISCUSSION

In this study, we evaluated the associations between temperature and rainfall, and the movement of flatwoods salamanders in and out of their breeding wetlands. We see movements concentrated in October on rainy nights over a specific range of ambient temperatures. Drawing from multiple, interacting environmental cues in this fashion may be an adaptive trait to avoid moving during heavy summer rains frequent in the southeastern US. Alternatively, salamanders may concentrate movements on nights with low temperatures when snake predators may be less active and/or when energetic stressors are lower. We were unable to disentangle the effects of absolute temperatures from relative changes in temperature. The importance of changing temperatures, as opposed to temperature per se, has recently been demonstrated in avian nesting behavior (Schaper et al.,

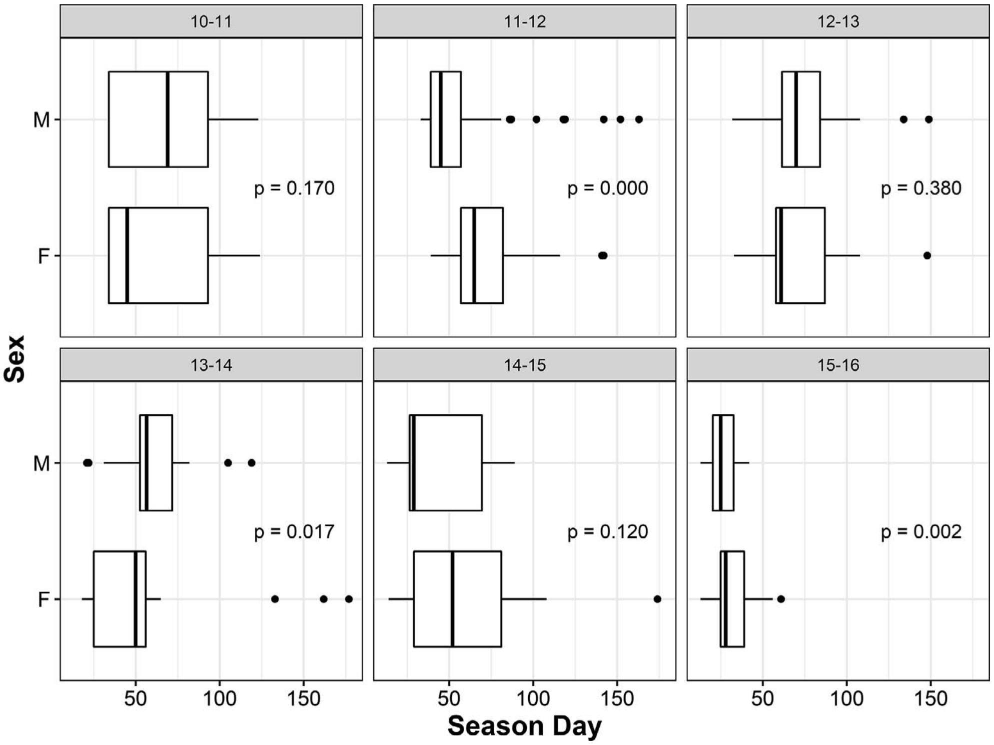

Fig. 2. Comparison of arrival dates for male and female flatwoods salamanders. Plots are standardized from 1 October and separated by year, i.e., 10–11 is the fall 2010–spring 2011 breeding season. Within year comparisons are made with Wilcoxon rank-sum tests.

2012); we predict similar mechanisms operate in many amphibian phenologies and deserve further study.

We also found a significant effect of date on salamander movements. Date can serve as a proxy for photoperiod or reflect any number of endogenous cues decoupled from environmental conditions (Both et al., 2008; Canavero et al., 2008). Whilst such endogenous cues to migration behavior are commonly acknowledged in mammals and birds (Knudsen et al., 2011; Williams et al., 2014), they are not as well documented in analogous amphibian research (Bradshaw and Holzapfel, 2007; but see Grant et al., 2009 and references therein). The negative relationship between date and daily counts stems from the synchronous arrivals of individuals at the start of the breeding season, contrasting with the staggered, protracted departure of individuals subsequent to breeding. Although not categorized as an explosive breeder (Petranka, 1998), pulse movement events comprising a large proportion of the total population are still evident; half of all captures occurred on just 24 sampling nights.

Protandry, that is, the arrival of males before females at breeding sites, has been documented in several species within Ambystomatidae (Douglas, 1979; Semlitsch, 1985; Sexton et al., 1990; Semlitsch et al., 1993; Trenham et al., 2000). It has been suggested that males arriving early maximize the number of potential mating opportunities, especially when female arrivals are unpredictable. In contrast, females that defer arrival at breeding sites maximize mate choice (Morbey and Ydenberg, 2001). Our results provide evidence of protandry in flatwoods salamanders. However, males only preceded females in two years of our study. For the remaining years, synchrony in arrival times of male and females occurred in the 2010–2011, 2012–2013, and 2014–2015 seasons, corroborating the observations of Palis (1997), and females arrived earlier than males in the 2013–2014 season.

It has been suggested that unpredictable resources, and the high probability of reproductive failure, selects for synchronous arrivals in ephemeral pool breeders (Dodd, 1993; Hartel et al., 2007). This is certainly an apt description of flatwoods salamander ecology, with only two successful recruitment years over the course of this study. Alternatively, synchronization can be attributed to sperm competition or other sexual behaviors, as shown in *Triturus* spp. (Hartel et al., 2007). Neither of these mechanisms, however, can explain variability across years in the timing of movement when comparing males and females. To the authors' knowledge, this is the first documentation of such inter-annual variability in arrival times for any pond-breeding amphibian. It is possible that in dry summers, some adults remain in the breeding ponds so are not detected immigrating in the following season. Additionally, after multiple years of reproductive failure, the adult population declines, and differential mortality by sex or small sample size may contribute to the difficulty in discerning patterns. More research on the relationship between environmental stochasticity and synchrony is needed.

A better understanding of the environmental factors driving migration is important for conservation and management of species of amphibians that make seasonal movements. Such studies also contribute to our basic knowledge of amphibian behavior and phenotypic constraints. Amphibian populations can suffer heavy mortality when they cross roads to move between their terrestrial and breeding habitats, and several mitigation strategies (such as temporary road closures or citizen volunteer "bucket-brigade" transport) depend on an ability to predict timing of amphibian movement (Schmidt and Zumbach, 2008; Beebee, 2013). In addition, evaluating whether a particular wetland has a suitable hydroperiod for a species of concern, or determining the temporal niches of different species of amphibians breeding in the same wetland, requires information on the timing of arrival and departure (Paton and Crouch, 2002).

Amphibian conservation operates on a relative shoestring budget, and intensive long-term monitoring is often unsustainable (Beebee, 2014; Walls et al., 2017; Meredith et al., 2018). Future sampling efforts should be tailored to maximize capture rates with the minimum cost. The negative binomial model provided useful threshold limits for precipitation and temperature beyond which salamander movement is likely, and identified a 'Goldilocks' set of environmental conditions that flatwoods salamanders favor. No captures were made on nights where temperature exceeded 22°C or fell below –1.5°C. Similarly, nights with more than ten captures did not occur before 25 October or after 25 February. This kind of information can be used to inform managers as to when surveys should be conducted and when monitoring can be curtailed with negligible loss of data. More broadly, the analytical tools described above can be employed in any study of pond-breeding amphibians to develop a more cost-effective monitoring schedule.

The strong association between climatic variables and salamander movement foreshadows future challenges in the face of climate change for this endangered species. Rising temperatures may delay arrival times at breeding wetlands (as shown for two species of salamander by Todd et al., 2011), thereby reducing the amount of time available for larval development. With climate projections forecasting more sporadic rainfall events over the species range (Mulholland et al., 1997; Chandler et al., 2016), the timing of salamander movements will likely become decoupled from environmental conditions conducive to successful reproduction; given enough change, those conditions may cease to exist entirely. The impacts of this phenological mismatch are predicted to be extremely detrimental to long-term population viability (Jakob et al., 2003; Chandler et al., 2016). Indeed, the annual variability in protandry seen in these populations may reflect maladaptive consequences of environmental perturbations that have already occurred.

Amphibians are often considered amongst vertebrates the most at risk to climate change (Alford, 2010). To date, the relative contributions of climatic cues and circannual rhythms to amphibian phenologies has received little attention, yet in order to confidently predict the response of amphibians to future climate scenarios, the degree of plasticity in phenological traits needs to be addressed. Experimental work on the proximate drivers of movement would help to this end. To combat the bleak prospects that amphibians face, the methods described herein allow researchers to exercise thrift, both in terms of sampling design and survey effort, and shrewdness in their mitigation strategies.

DATA ACCESSIBILITY

Supplemental information is available at https://www.copeiajournal.org/ch-18-068.

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