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Abstract

The spatial covariance between prey and predator densities is closely related to the rate of encounters, and thus to predation rates. To include the effect of covariance in dynamic predator–prey models it is useful to express the spatial covariance as a function of predator and prey densities. Here we derive mean–covariance relationships for a scenario where predators show an aggregative response, i.e., they respond behaviorally by aggregating in patches with high prey densities. Prey, on the other hand, do not respond to predator densities. Some explicit expressions are obtained when the prey distribution is clumped or random. It is shown that the prey-predator covariance can be expressed only through the distributional information of prey. In particular when the prey distribution is clumped or random, this covariance depends only on the mean prey density.

Keywords: Predator-prey interaction, covariance, aggregative response, negative binomial distribution, Poisson distribution.

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1 Introduction

Models describing the consumptive interactions between predators and prey typically assume that systems are well mixed, and thus that the rate of encounters between predators and prey are proportional to mean densities of predators and prey. Most natural systems are not well mixed; predators and prey typically have clumped and correlated spatial distributions. The effect of the correlation between the two distributions on predation rates can be described using the spatial covariance between predator and prey densities. For example, it can be shown for a linear functional response that the numbers consumed by predators (E) per unit area is given by $E = a\bar{N}\bar{P} + a\sigma_{NP}$, where a is the search efficiency in a well mixed system, \bar{N} and \bar{P} are mean prey and predator densities, and σ_{NP} is the covariance between predator and prey densities (Bergström et al. 2006).

The functional response equation is a fundamental part of dynamic models of predator-prey interactions. Such models typically use coupled differential equations to describe the change in predator and prey densities as functions of mean densities. To include the effects of the covariance in such models it is therefore useful to express the covariance as a function of average densities. Thus it is motivated to investigate if the covariance can be described as a function of average predator and prey densities. Here we investigate a scenario where predators show an aggregative response, i.e., they respond behaviorally by aggregating in patches with high prey densities. Prey, on the other hand, do not respond to predator densities. This corresponds to a situation where predators are much more mobile than their prey, e.g., herbivores feeding on plants or parasitoids attacking eggs.

In next section the prey-predator covariance structure is established for a situation when predators have an aggregative response to prey densities. Some explicit expressions are obtained when the prey distribution is clumped or random. Conclusions and discussions can be found in Section 3. All the proofs are left in the Appendix.

2 Models and results

In this section we consider the relationship between the local density of prey and predators when predators show an aggregative response, i.e., they aggregate in high patches with high prey densities. More specifically, the covariance structure given different types of aggregative responses will be investigated.

Let X and Y be the number (density) of prey and predators in a patch at a given point in time. Some notations need to be introduced:

$p(x) = \mathbb{P}[X = x]$: the probability that a patch is inhabited by exactly x prey,
 $x = 0, 1, \dots$

$p(y|x) = \mathbb{P}[Y = y|X = x]$: the conditional probability that patches with x prey are occupied by y predators, $y = 0, 1, \dots$

$\mu_X = \mathbb{E}[X]$: the expectation of X ,

$\mu_Y = \mathbb{E}[Y]$: the expectation of Y ,

$\mu_{Y|X} = \mathbb{E}[Y|X]$: the conditional expectation of Y given X ,

$\sigma_X^2 = \mathbb{E}[X - \mathbb{E}[X]]^2$: the variance of X ,

$\sigma_Y^2 = \mathbb{E}[Y - \mathbb{E}[Y]]^2$: the variance of Y .

By using the conditional expectation $\mu_{Y|X}$, we can get the following expression of the covariance between prey and predator:

$$\begin{aligned} \text{Cov}(X, Y) &= \mathbb{E}[XY] - \mathbb{E}[X] \cdot \mathbb{E}[Y] \\ &= \mathbb{E}[X \cdot \mathbb{E}[Y|X]] - \mathbb{E}[X] \cdot \mathbb{E}[\mathbb{E}[Y|X]] \\ &\triangleq \mathbb{E}[X\mu_{Y|X}] - \mu_X \cdot \mathbb{E}[\mu_{Y|X}]. \end{aligned} \quad (2.1)$$

It can be seen from (2.1) that the covariance is only depending on the information about predator number through the conditional expectation $\mu_{Y|X}$, besides the distributional information of prey, which implies that calculation of the prey-predator covariance does not require the entire distributional information for the predators. This property motivates us to investigate the prey-predator covariance by utilizing the aggregative response model, because the latter describes precisely how the conditional expectation varies with the prey density.

As a general model of aggregative responses Nachman (2006) proposed that the expected number of predators inhabiting a patch with x prey is given by:

$$\frac{d\mu_{Y|X=x}}{dx} = cx^m e^{\lambda x}, \quad (2.2)$$

where m, c and λ are species specific parameters describing the shape of the aggregative response. m is either 0 or 1, c is either 0 (i.e. no aggregative response) or positive (i.e. the number of predators is positively associated with the number of prey per patch). The higher the value of c , the more will the predators tend to aggregate in patches with abundant prey, whereas $\mu_{Y|X=x}$ will decrease in patches with few prey. These parameters can be estimated by

simultaneously fitting the response model to the associated values of X and Y using the maximum likelihood method.

There are five main types of aggregative response (Van der Meer and Ens, 1997) that can be derived from model (2.2):

- (i) $c = 0$: the predators do not show any aggregative response;
- (ii) $c > 0, m = 0, \lambda = 0$: the aggregative response increases linearly with prey density;
- (iii) $c > 0, m = 1, \lambda = 0$: the response accelerates with prey density;
- (iv) $c > 0, m = 0, \lambda < 0$: the response increase with decelerating slope and approaches an upper asymptote;
- (v) $c > 0, m = 1, \lambda < 0$: the response is sigmoid.

Type (ii), (iv) and (v) correspond to what Gascoigne and Lipcius (2004) classified as type I, II and III aggregative response, respectively. General solutions for $\mu_{Y|X=x}$ can be found in Nachman (2006, Appendix 1).

From the general expression of prey-predator covariance (2.1) we derive specific expressions corresponding to each of the five aggregative response models.

Proposition 1. *The covariance between prey and predators can be expressed in accordance to the types of aggregative response as follows:*

- (i) $Cov(X, Y) = 0$;
- (ii) $Cov(X, Y) = c \sigma_X^2$;
- (iii) $Cov(X, Y) = \frac{c}{2} \mathbb{E} [X^3 - \mu_X X^2]$;
- (iv) $Cov(X, Y) = \frac{c}{\lambda} \mathbb{E} [(X - \mu_X)e^{\lambda X}]$;
- (v) $Cov(X, Y) = \frac{c}{\lambda} \mathbb{E} \left[(X^2 - (\mu_X + \frac{1}{\lambda})X + \frac{\mu_X}{\lambda})e^{\lambda X} \right]$.

Remark 1: This proposition tells us that the prey-predator covariance does not depend on the expectation of the predator density, no matter which aggregative response model we choose. Actually no distributional information of the predator density is needed.

Remark 2: If the expected predator density (given a prey density) is a linear increasing function of prey density as in model (ii), the prey-predator covariance is proportional to the prey variance, irrespective of the shape of the prey

and predator distributions. Therefore, it is always positive. It is also interesting to observe that the prey-predator correlation in this case is proportional to the ratio of standard deviations between prey and predator, that is,

$$\text{Corr}(X, Y) = c \frac{\sigma_X}{\sigma_Y}.$$

Remark 3: For the model of accelerating aggregative responses (iii), the covariance is a function of the first three moments of prey density. Specifically,

$$\text{Cov}(X, Y) = \frac{c}{2} \sigma_X^3 \gamma_X + c \mu_X \sigma_X^2,$$

where γ_X denotes the skewness of prey density.

Remark 4: For convex and sigmoid aggregative responses (models (iv) and (v)), the covariance can be described by means of the moment generating function (m.g.f.) of prey density and its derivatives. In fact, denoting by $M_X(\lambda)$ the m.g.f. for prey density X , we have

$$\text{Cov}(X, Y) = \begin{cases} \frac{c}{\lambda} [M'_X(\lambda) - \mu_X M_X(\lambda)], & \text{for convex;} \\ \frac{c}{\lambda} \left[M''_X(\lambda) - (\mu_X + \frac{1}{\lambda}) M'_X(\lambda) + \frac{\mu_X}{\lambda} M_X(\lambda) \right], & \text{for sigmoid.} \end{cases}$$

Note that $M_X(\lambda)$ exists for $\lambda \leq 0$ since X is a nonnegative integer-valued random variable.

The prey-predator covariance becomes more explicit if the prey distribution is specified. Here we consider the two different types of prey distribution as in Nachman (2006): clumped and random. Note that the case of no aggregative response, i.e. model (i), is omitted.

2.1 Clumped prey distribution

When the prey distribution is clumped, that is, X is negativ binomial distributed (NBD), its probability function is known as

$$p(x) = \mathbb{P}[X = x] = \frac{\Gamma(x+r)}{x! \Gamma(r)} p^r q^x, \quad (2.3)$$

where $p = 1 - q = r/(\mu_X + r)$. $\mu_X = rq/p$ is the mean number of individuals per unit and r is a parameter expressing the degree of clumping. The variance of the NBD is given as $\sigma_X^2 = \mu_X + \mu_X^2/r$, which is always larger than the mean μ_X , corresponding to the over-dispersed Poisson distribution. The advantage

of using the NBD is that it allows for any degree of aggregation ranging from a random (Poisson) distribution (when $r \rightarrow \infty$) to an extremely clumped distribution (when $r \rightarrow 0$).

From Proposition 1 we obtain the covariance expression for the clumped prey distribution.

Proposition 2 (Clumped). *Suppose that the prey density obeys NBD with parameter r . Then the prey-predator covariance can be expressed in accordance to the types of aggregative response as follows:*

$$\begin{aligned}
\text{(ii)} \quad \text{Cov}(X, Y) &= c \mu_X \left[1 + \frac{\mu_X}{r} \right]; \\
\text{(iii)} \quad \text{Cov}(X, Y) &= c \mu_X \left[1 + \frac{\mu_X}{r} \right] \left[\frac{1}{2} + \mu_X + \frac{\mu_X}{r} \right]; \\
\text{(iv)} \quad \text{Cov}(X, Y) &= c \mu_X \left[1 + \frac{\mu_X}{r} \right] \frac{(e^\lambda - 1)}{\lambda} \left[1 + \frac{\mu_X}{r} (1 - e^\lambda) \right]^{-(r+1)}; \\
\text{(v)} \quad \text{Cov}(X, Y) &= \frac{c \mu_X}{\lambda^2} \left[1 + \frac{\mu_X}{r} \right] \left[\left(1 - \mu_X \left(\lambda + \frac{1}{r} \right) e^\lambda + \frac{\mu_X}{r} \right) (1 - e^\lambda) + \lambda e^\lambda \right] \\
&\quad \times \left[1 + \frac{\mu_X}{r} (1 - e^\lambda) \right]^{-(r+2)}.
\end{aligned}$$

Remark 5: Proposition 2 shows that the prey-predator covariance, when prey distribution is clumped, is simplified to a function of the mean prey density and the clumping parameter, besides the shape parameter λ in the aggregative response model. Furthermore, the covariance is positive, except for the sigmoid response model. The more prey is clumped, the larger the covariance is. In another words, the prey-predator covariance decreases as the prey density is distributed more randomly.

Remark 6: It is obvious that the prey-predator covariance is a polynomial function of the mean prey density μ_X for model (ii) and (iii). This is also true for the convex and sigmoid aggregative response models when the expected value of prey density is high. In fact, the covariance is approximately proportional to μ_X^{1-r} , if μ_X is large.

2.2 Random prey distribution

As the extreme case, when the clumping parameter goes to infinite, we get the covariance structure for the random prey distribution.

When $r \rightarrow \infty$, it follows from (2.3) that

$$p(x) = \frac{\Gamma(x+r)}{x!\Gamma(r)} p^r q^x = \frac{\mu_X^x}{x!} \frac{\Gamma(r+x)}{\Gamma(r)(r+\mu_X)^x} \left(1 + \frac{\mu_X}{r}\right)^{-r} \rightarrow \frac{\mu_X^x}{x!} e^{-\mu_X}.$$

The parameter r controls the deviation from Poisson. This makes the NBD suitable as a robust alternative to the Poisson, which approaches the Poisson for large r , but which has larger variance than the Poisson for small r .

From Proposition 2 we have the following expression of the prey-predator covariance.

Proposition 3 (Random). *Suppose that the prey density obeys Poisson distribution. Then the prey-predator covariance can be expressed in accordance to the types of aggregative response as follows:*

(ii) $Cov(X, Y) = c \mu_X;$

(iii) $Cov(X, Y) = \frac{c}{2} [\mu_X + 2\mu_X^2];$

(iv) $Cov(X, Y) = \frac{c\mu_X}{\lambda} (e^\lambda - 1) e^{-\mu_X(1-e^\lambda)};$

(v) $Cov(X, Y) = \frac{c\mu_X}{\lambda^2} \left[(1 - \mu_X \lambda e^\lambda)(1 - e^\lambda) + \lambda e^\lambda \right] e^{-\mu_X(1-e^\lambda)}.$

Remark 7: It can be seen that the prey-predator covariances is always positive when the prey density is randomly distributed.

3 Conclusion and discussion

The prey-predator covariance is important for characterizing the dynamics of predator-prey systems that are spatially heterogeneous. For example, a positive covariance between hosts and parasitoids can stabilize otherwise unstable dynamics (see Murdoch et al. 2005). In other systems, such as the benthic predator-prey system described by Bergström et al. (2006), it was found that the covariance instead destabilized the dynamics. It should be noted though, that the covariance can only be viewed as a variable that controls population dynamics if it is generated by processes that are not dynamically coupled to birth and mortality, i.e., the processes that drives population dynamics. Examples of such situations are when the covariance is generated by spatial variation in habitat quality, or when there is a clear separation of time scales between movement responses and those of birth and mortality. In contrast, in

systems with unstable mean dynamics, it is the rule that also the covariance and other higher order moments exhibit oscillating dynamics. In this situation the covariance should be viewed not as driver, but as one of many descriptors, along with mean, variance etc., of the spatial dynamics of the system.

The results generated here apply to situations when predators aggregate in response to high prey densities. The response should be driven by predator movements and be expressed on a time scale that is fast compared to the rate of birth and mortality. For this situation we have derived relatively simple mean-covariance relationships that can be incorporated in spatial predator-prey models. In particular we note that for linear aggregative responses the covariance is expected to be proportional to the spatial variance of prey density. It is a well supported empirical generalization in population ecology that variances can be described by a power function of mean densities, suggesting that empirical covariances often can be approximated by a power function of mean prey density as long as the aggregative response is approximately linear.

In general, for different types of predator aggregative responses (including linearly increasing, accelerating, increasing with decelerating slope and approaching an upper asymptote, and sigmoid), the prey-predator covariance can be expressed using only information about the prey density distribution. In particular, when prey distribution is clumped, the covariance is a polynomial function of the mean prey density when the aggregative response is linear or accelerating. This is also true for the convex and sigmoid aggregative response models when the expected value of prey density is high.

An analogous scenario is expected in situations when prey avoid areas with high predator densities which, if prey are more mobile than predators, should generate a negative relationship between predator and prey densities. This situation will be analyzed in a forthcoming report.

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A Proof of Proposition 1

Proof. We derive the prey-predator covariance structure for each aggregative response model.

Model (i) This simplest case implies that $\mu_{Y|X=x} = \mu_Y$ and no response from the predators. Thus $Cov(X, Y) = 0$.

Model (ii) In this case, the aggregative response model simply leads to

$$\mu_{Y|X=x} = \mu_Y + c(x - \mu_X); \quad c \leq \frac{\mu_Y}{\mu_X}.$$

Plugging it into (2.1) results to

$$\begin{aligned} Cov(X, Y) &= \mathbb{E}[X\mu_{Y|X}] - \mu_X \cdot \mathbb{E}[\mu_{Y|X}] \\ &= \mu_X \cdot \mu_Y + c\mathbb{E}[X^2] - c(\mu_X)^2 - \mu_X \cdot \mu_Y \\ &= c \sigma_X^2. \end{aligned} \tag{A.1}$$

Model (iii) The general solution to this model is

$$\mu_{Y|X=x} = \mu_Y + \frac{c}{2} (x^2 - \mathbb{E}[X^2]); \quad c \leq \frac{2\mu_Y}{\mathbb{E}[X^2]}.$$

From (2.1) it follows that

$$\begin{aligned} Cov(X, Y) &= \mathbb{E}[X\mu_{Y|X}] - \mu_X \cdot \mathbb{E}[\mu_{Y|X}] \\ &= \mathbb{E} \left[X \left(\mu_Y + \frac{c}{2} (X^2 - \mathbb{E}[X^2]) \right) \right] - \mu_X \mathbb{E} \left[\mu_Y + \frac{c}{2} (X^2 - \mathbb{E}[X^2]) \right] \\ &= \frac{c}{2} \mathbb{E} [X^3 - \mu_X X^2]. \end{aligned} \tag{A.2}$$

Model (iv) The general solution of the aggregative response model here is

$$\mu_{Y|X=x} = \mu_Y + \frac{c}{\lambda} \left(e^{\lambda x} - \mathbb{E}[e^{\lambda X}] \right); \quad c \leq \frac{\lambda \mu_Y}{\mathbb{E}[e^{\lambda X}] - 1}.$$

Plugging it into (2.1) results to

$$\begin{aligned} Cov(X, Y) &= \mathbb{E}[X\mu_{Y|X}] - \mu_X \cdot \mathbb{E}[\mu_{Y|X}] \\ &= \mathbb{E} \left[X \cdot \left(\mu_Y + \frac{c}{\lambda} (e^{\lambda X} - \mathbb{E}[e^{\lambda X}]) \right) \right] - \mu_X \mathbb{E} \left[\mu_Y + \frac{c}{\lambda} (e^{\lambda X} - \mathbb{E}[e^{\lambda X}]) \right] \\ &= \frac{c}{\lambda} \left(\mathbb{E}[X e^{\lambda X}] - \mu_X \mathbb{E}[e^{\lambda X}] \right) \\ &= \frac{c}{\lambda} \mathbb{E} \left[(X - \mu_X) e^{\lambda X} \right]. \end{aligned} \tag{A.3}$$

Model (v) The general solution to the last type of aggregative response model is

$$\mu_{Y|X=x} = \mu_Y + \frac{c}{\lambda} \left(xe^{\lambda x} - \mathbb{E}[Xe^{\lambda X}] - \frac{1}{\lambda}(e^{\lambda x} - \mathbb{E}[e^{\lambda X}]) \right),$$

where $c \leq \frac{\lambda^2 \mu_Y}{\lambda \mathbb{E}[Xe^{\lambda X}] - \mathbb{E}[e^{\lambda X}] + 1}$. Plugging it into (2.1) results to

$$\begin{aligned} \text{Cov}(X, Y) &= \mathbb{E}[X\mu_{Y|X}] - \mu_X \cdot \mathbb{E}[\mu_{Y|X}] \\ &= \mathbb{E} \left[X \cdot \left(\mu_Y + \frac{c}{\lambda} \left(xe^{\lambda x} - \mathbb{E}[Xe^{\lambda X}] - \frac{1}{\lambda}(e^{\lambda x} - \mathbb{E}[e^{\lambda X}]) \right) \right) \right] \\ &\quad - \mu_X \cdot \mathbb{E} \left[\mu_Y + \frac{c}{\lambda} \left(xe^{\lambda x} - \mathbb{E}[Xe^{\lambda X}] - \frac{1}{\lambda}(e^{\lambda x} - \mathbb{E}[e^{\lambda X}]) \right) \right] \\ &= \frac{c}{\lambda} \left(\mathbb{E}[X^2 e^{\lambda X}] - \mu_X \cdot \mathbb{E}[Xe^{\lambda X}] - \frac{1}{\lambda} \mathbb{E}[Xe^{\lambda X}] + \frac{\mu_X}{\lambda} \mathbb{E}[e^{\lambda X}] \right) \\ &= \frac{c}{\lambda} \mathbb{E} \left[\left(X^2 - \left(\mu_X + \frac{1}{\lambda} \right) X + \frac{\mu_X}{\lambda} \right) e^{\lambda X} \right]. \end{aligned} \tag{A.4}$$

□

B Proof of Proposition 2

Proof. When the prey distribution is NBD, that is $X \sim NB(r, p)$, its moments are given as follows.

$$\mu_X = \mathbb{E}[X] = \frac{rq}{p}, \quad (\text{B.1})$$

$$\mathbb{E}[X^2] = \frac{rq(1+rq)}{p^2} = \mu_X \left[1 + \mu_X + \frac{\mu_X}{r} \right], \quad (\text{B.2})$$

$$\sigma_X^2 = \frac{rq}{p^2} = \mu_X \left[1 + \frac{\mu_X}{r} \right], \quad (\text{B.3})$$

$$\begin{aligned} \mathbb{E}[X^3] &= \frac{rq[1+q+3rq+r^2q^2]}{p^3} \\ &= \mu_X \left[1 + \frac{\mu_X}{r} \right] \left[1 + \left(3 + \frac{2}{r} + \frac{r\mu_X}{r+\mu_X} \right) \mu_X \right], \end{aligned} \quad (\text{B.4})$$

$$\mathbb{E}[e^{\lambda X}] = \left[1 + \frac{\mu_X}{r}(1-e^\lambda) \right]^{-r}, \quad (\text{B.5})$$

$$\mathbb{E}[Xe^{\lambda X}] = \mu_X e^\lambda \left[1 + \frac{\mu_X}{r}(1-e^\lambda) \right]^{-(r+1)}, \quad (\text{B.6})$$

$$\begin{aligned} \mathbb{E}[X^2 e^{\lambda X}] &= \sigma_X^2 e^\lambda (1+rqe^\lambda) \left[1 + \frac{\mu_X}{r}(1-e^\lambda) \right]^{-(r+2)} \\ &= \mu_X e^\lambda \left(1 + \frac{\mu_X}{r} + \mu_X e^\lambda \right) \left[1 + \frac{\mu_X}{r}(1-e^\lambda) \right]^{-(r+2)}. \end{aligned} \quad (\text{B.7})$$

Type (ii) From Proposition 1(ii) it is seen that

$$\text{Cov}(X, Y) = c \sigma_X^2 = \frac{crq}{p^2} = c \mu_X \left[1 + \frac{\mu_X}{r} \right] \quad (\text{B.8})$$

Type (iii) From Proposition 1(iii) and (B.1)–(B.4) it follows that

$$\begin{aligned} \text{Cov}(X, Y) &= \frac{c}{2} \mathbb{E}[X^3 - \mu_X X^2] \\ &= \frac{c}{2} \left[\frac{rq[1+q+3rq+r^2q^2]}{p^3} - \frac{rq}{p} \cdot \frac{rq(1+rq)}{p^2} \right] \\ &= \frac{crq[1+q+2rq]}{2p^3} \\ &= c \mu_X \left[1 + \frac{\mu_X}{r} \right] \left[\frac{1}{2} + \mu_X + \frac{\mu_X}{r} \right]. \end{aligned} \quad (\text{B.9})$$

Type (iv) From Proposition 1(iv) together with (B.1)–(B.6) it follows that

$$\begin{aligned}
Cov(X, Y) &= \frac{c}{\lambda} \mathbb{E} \left[(X - \mu_X) e^{\lambda X} \right] \\
&= \frac{c}{\lambda} \left[\mu_X e^\lambda \left(1 + \frac{\mu_X}{r} (1 - e^\lambda) \right)^{-(r+1)} - \mu_X \left(1 + \frac{\mu_X}{r} (1 - e^\lambda) \right)^{-r} \right] \\
&= \frac{c}{\lambda} \mu_X \left[e^\lambda - \left(1 + \frac{\mu_X}{r} (1 - e^\lambda) \right) \right] \left[1 + \frac{\mu_X}{r} (1 - e^\lambda) \right]^{-(r+1)} \\
&= \frac{c}{\lambda} \mu_X (e^\lambda - 1) \left(1 + \frac{\mu_X}{r} \right) \left[1 + \frac{\mu_X}{r} (1 - e^\lambda) \right]^{-(r+1)} \\
&= \frac{crq(e^\lambda - 1)}{p^2 \lambda} \left[1 + \frac{q}{p} (1 - e^\lambda) \right]^{-(r+1)} \\
&= c \mu_X \left[1 + \frac{\mu_X}{r} \right] \frac{(e^\lambda - 1)}{\lambda} \left[1 + \frac{\mu_X}{r} (1 - e^\lambda) \right]^{-(r+1)}. \tag{B.10}
\end{aligned}$$

Type (v) From Proposition 1(v) together with (B.1)–(B.7) it follows that

$$\begin{aligned}
Cov(X, Y) &= \frac{c}{\lambda} \mathbb{E} \left[\left(X^2 - \left(\mu_X + \frac{1}{\lambda} \right) X + \frac{\mu_X}{\lambda} \right) e^{\lambda X} \right] \\
&= \frac{c}{\lambda} \left(\mathbb{E}[X^2 e^{\lambda X}] - \left(\mu_X + \frac{1}{\lambda} \right) \mathbb{E}[X e^{\lambda X}] + \frac{\mu_X}{\lambda} \mathbb{E}[e^{\lambda X}] \right) \\
&= \frac{c}{\lambda} \left\{ \sigma_X^2 e^\lambda (1 + r q e^\lambda) \left[1 + \frac{\mu_X}{r} (1 - e^\lambda) \right]^{-(r+2)} - \right. \\
&\quad \left. - \left(\mu_X + \frac{1}{\lambda} \right) \mu_X e^\lambda \left[1 + \frac{\mu_X}{r} (1 - e^\lambda) \right]^{-(r+1)} + \right. \\
&\quad \left. + \frac{\mu_X}{\lambda} \left[1 + \frac{\mu_X}{r} (1 - e^\lambda) \right]^{-r} \right\} \\
&= \frac{c}{\lambda} \frac{r q}{\lambda p^3} \left[1 + \frac{\mu_X}{r} (1 - e^\lambda) \right]^{-(r+2)} \times \\
&\quad \times \left[\lambda p e^\lambda (1 + r q e^\lambda) - (\lambda r q + p) (e^\lambda - q e^{2\lambda}) + (1 - q e^\lambda)^2 \right] \\
&= \frac{c}{\lambda} \frac{r q}{\lambda p^3} \left[1 + \frac{q}{p} (1 - e^\lambda) \right]^{-(r+2)} \times \\
&\quad \times \left[1 + [(\lambda p - 1) - q(\lambda r + 1)] e^\lambda + [\lambda r + 1] q e^{2\lambda} \right] \\
&= \frac{c r q}{\lambda^2 p^3} \left[\left((\lambda r + 1) q e^\lambda - 1 \right) (e^\lambda - 1) + \lambda p e^\lambda \right] \left[1 + \frac{q}{p} (1 - e^\lambda) \right]^{-(r+2)} \\
&= \frac{c \mu_X}{\lambda^2} \left[1 + \frac{\mu_X}{r} \right] \left[\left(\mu_X \left(\lambda + \frac{1}{r} \right) e^\lambda - \frac{\mu_X}{r} - 1 \right) (e^\lambda - 1) + \lambda e^\lambda \right] \\
&\quad \times \left[1 + \frac{\mu_X}{r} (1 - e^\lambda) \right]^{-(r+2)}. \tag{B.11}
\end{aligned}$$

□