

Exact Distributional Results for Random Resistance Trees¹

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ABSTRACT. With a view to the study of, for instance, arterial trees, this paper presents some exact distributional results on finite trees with (reciprocal) inverse Gaussian and gamma resistances. In particular, it is shown that under the specified model the conditional distribution of the minimal sufficient statistic given the total resistance of the tree is a convolution of gamma distributions and two-dimensional reciprocal inverse Gaussian distributions.

Key words: exponential models; multivariate (reciprocal) inverse Gaussian laws.

1 Introduction

Networks with random resistances (or, equivalently, random conductivities) have been the object of extensive study in both mathematics and physics. Some key references are Stinchcombe (1974), Kesten (1982), Grimmet (1993), Soardi (1994) and Lyons & Peres (1998).

In the context of physics, much of the literature has been concerned with critical phenomena, typically for infinite networks with independent identically distributed resistances on the edges, a key question being whether the total resistance of the network is infinite or not. For the study of, for instance, arterial networks results of the kind indicated are generally of little relevance. In particular, the assumption of identically distributed resistances is clearly inappropriate and, furthermore, the question of infinite total resistance does not arise. For some

¹Revised and expanded version of a manuscript that appeared as Research Report 379 (1997) from Dept. Theor. Statist., Univ. Aarhus.

²Centre for Mathematical Physics and Stochastics – funded by The Danish National Research Foundation.

interesting recent work on blood flow and growth of arterial trees, see Bassingthwaite, King & Roger (1989), Mayrovitz & Roy (1983), Sandau & Kurz (1993), Schmid-Schoenbein, Firestone & Zweifach (1986), Sun, Meakin & Jossang (1995) and VanBavel & Spaan (1992). Of special interest are the physiological mechanisms by which the pressure drop throughout the arterial tree is regulated. Up to 50% or more of the peripheral resistance appears to lie proximal to vessels with diameter of $100 \mu m$ (Mulvany & Aalkjær 1990). This led us to consider resistance trees with several levels of constant potential, cf. Section 4. Our results can conceivably be used to identify changes in parameters describing the pressure at different levels of the arterial network.

The present paper is part of a wider study (cf. Barndorff-Nielsen (1994), Barndorff-Nielsen & Koudou (1998), Barndorff-Nielsen & Rydberg (1998)) aimed at building statistically tractable parametric models for networks such as arterial trees. A key basis for this work has been the observation that the properties of the inverse Gaussian and the reciprocal inverse Gaussian distributions fit together, in a quite unique way, with the elementary Kirchoff-Ohms laws. Using those distributions, it is possible to build rather versatile and simple exponential models, a particular aspect of these being that the total resistance follows a reciprocal inverse Gaussian distribution. This property, which is one of a very few exact distributional results in the theory of random resistance networks, allows one to obtain further exact distributional properties of the conditional law given the total resistance, the latter often being an observable quantity. A first such conditional result was given in Barndorff-Nielsen & Koudou (1998) and the present paper generalizes this. As an unexpected byproduct, a bivariate reciprocal inverse Gaussian distribution, previously considered purely on grounds of mathematical simplicity, is seen to occur naturally in the present biologically motivated context.

Section 2 summarizes some basic results concerning the inverse, reciprocal and generalized inverse Gaussian distributions, and the relation to the Kirchoff-Ohms laws is indicated. Section 3 sets up definitions and notation for the random resistance trees to be studied and the new distributional results are derived and explained in more detail in Section 4.

2 *IG, RIG and GIG distributions*

The generalized inverse Gaussian distribution $GIG(\lambda, \delta, \gamma)$ has density function

$$gig(x; \lambda, \delta, \gamma) = \frac{(\gamma/\delta)^\lambda}{2K_\lambda(\delta\gamma)} x^{\lambda-1} \exp\left(-\frac{1}{2}(\delta^2 x^{-1} + \gamma^2 x)\right), \quad x > 0, \quad (1)$$

where the domain of variation of $(\lambda, \delta, \gamma)$ is given by

$$\begin{aligned} \delta \geq 0 \quad \gamma > 0 & \quad \text{if} \quad \lambda > 0, \\ \delta > 0 \quad \gamma > 0 & \quad \text{if} \quad \lambda = 0, \\ \delta > 0 \quad \gamma \geq 0 & \quad \text{if} \quad \lambda < 0, \end{aligned}$$

and where K_λ denotes the modified Bessel function of the third kind with index λ . In case $\delta = 0$ and $\gamma = 0$ the norming constant in (1) has to be interpreted in terms of the limit of $K_\lambda(y)$ for $y \downarrow 0$ (For relevant properties of the Bessel functions see e.g. the appendix of Jørgensen (1982)). The *GIG* distributions possess the property that

$$X \sim GIG(\lambda, \delta, \gamma) \iff X^{-1} \sim GIG(-\lambda, \gamma, \delta). \quad (2)$$

Furthermore, for every constant $a > 0$

$$X \sim GIG(\lambda, \delta, \gamma) \implies aX \sim GIG(\lambda, a^{1/2}\delta, a^{-1/2}\gamma). \quad (3)$$

The most prominent member of the family of *GIG* distributions is the inverse Gaussian $IG(\delta, \gamma) = GIG(-1/2, \delta, \gamma)$ with density function given by

$$ig(x; \delta, \gamma) = \frac{\delta}{\sqrt{2\pi}} e^{\delta\gamma} x^{-3/2} \exp\left(-\frac{1}{2}(\delta^2 x^{-1} + \gamma^2 x)\right).$$

The *IG* distribution has a probabilistic interpretation as the *first* hitting time to the level δ of a Brownian motion with drift γ and diffusion coefficient 1.

Using the relation in (2) leads from $IG(\delta, \gamma)$ to the reciprocal inverse Gaussian $RIG(\delta, \gamma) = GIG(1/2, \delta, \gamma)$ distribution with density function

$$rig(x; \delta, \gamma) = \frac{\gamma}{\sqrt{2\pi}} e^{\delta\gamma} x^{-1/2} \exp\left(-\frac{1}{2}(\delta^2 x^{-1} + \gamma^2 x)\right).$$

Like the *IG* distribution the *RIG* distribution can be given a probabilistic interpretation. In fact, the *RIG* distribution is the distribution of the *last* hitting time to the level δ of a Brownian motion with drift γ and diffusion coefficient 1, cf. Vallois (1991). These hitting time interpretations are of direct relevance for the type of models for resistances on trees considered in the following, see Barndorff-Nielsen & Koudou (1998).

The gamma (Γ) distribution is also in the family of *GIG* distributions. It is the special case where $\lambda > 0$ and $\delta = 0$, i.e. $GIG(\lambda, 0, \gamma) = \Gamma(\lambda, \gamma^2/2)$, and the density is then given by

$$\gamma \left(x; \lambda, \frac{\gamma^2}{2} \right) = \frac{(\gamma^2/2)^\lambda}{\Gamma(\lambda)} x^{\lambda-1} \exp \left(-\frac{1}{2} \gamma^2 x \right).$$

We have the following well known convolution properties of *GIG* random variables:

1. $\Gamma \left(\lambda_1, \frac{\gamma^2}{2} \right) * \Gamma \left(\lambda_2, \frac{\gamma^2}{2} \right) = \Gamma \left(\lambda_1 + \lambda_2, \frac{\gamma^2}{2} \right)$,
2. $IG(\delta_1, \gamma) * IG(\delta_2, \gamma) = IG(\delta_1 + \delta_2, \gamma)$,
3. $IG(\delta_1, \gamma) * RIG(\delta_2, \gamma) = RIG(\delta_1 + \delta_2, \gamma)$,
4. $GIG(-\lambda, \delta, \gamma) * \Gamma \left(\lambda, \frac{\gamma^2}{2} \right) = GIG(\lambda, \delta, \gamma)$ for every $\lambda > 0$.

Note that the properties 2. and 3. are immediate consequences of the above-mentioned hitting time interpretations.

These convolution results can be seen to correspond intimately with the Kirchoff–Ohm laws, the simplest form of which states that: If two networks with resistances R and R' are connected sequentially the total resistance is $R + R'$ while if they are connected in parallel the overall resistance is

$$\left(R^{-1} + R'^{-1} \right)^{-1}. \quad (4)$$

To give a graphical illustration of this consider the simple tree in Figure 1, which is described by the set of edges $\{e_1, e_2, e_3\}$ and the vertices $\{v_1, v_2\}$. Here the edges and vertices are equipped with random variables $X_{e_1}, X_{e_2}, X_{e_3}, X_{v_1}, X_{v_2}$ where

$$\begin{aligned} X_{e_1} &\sim IG(\psi_1, \chi), & X_{e_2} &\sim IG\left(\psi_2, \frac{3}{4}\chi\right), & X_{e_3} &\sim IG\left(\psi_2, \frac{1}{4}\chi\right) \\ X_{v_1} &\sim \Gamma\left(\frac{1}{2}, \frac{1}{2}\left(\frac{1}{4}\chi\right)^2\right), & X_{v_2} &\sim \Gamma\left(\frac{1}{2}, \frac{1}{2}\left(\frac{3}{4}\chi\right)^2\right). \end{aligned}$$

The two branches of the tree have resistances which by property 4. are given by

$$\begin{aligned} X_{e_2} + X_{v_2} &\sim RIG\left(\psi_2, \frac{3}{4}\chi\right), \\ X_{e_3} + X_{v_1} &\sim RIG\left(\psi_2, \frac{1}{4}\chi\right). \end{aligned}$$

By property 2. and the Kirchoff–Ohm law for parallelly connected resistances we see that the top part of the tree described by the edges $\{e_2, e_3\}$ and the vertices $\{v_1, v_2\}$ has resistance

$$\left((X_{e_2} + X_{v_2})^{-1} + (X_{e_3} + X_{v_1})^{-1} \right)^{-1} \sim RIG(\psi_2, \chi).$$

Finally, by using the rule for serially connected resistances and property 3. we get that the total resistance is

$$\left((X_{e_2} + X_{v_2})^{-1} + (X_{e_3} + X_{v_1})^{-1} \right)^{-1} + X_{e_1} \sim RIG(\psi_1 + \psi_2, \chi).$$

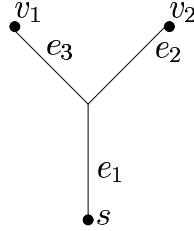


Figure 1: A tree with two branches.

In Barndorff-Nielsen, Blæsild & Seshadri (1992) the following results, which we will use in Section 4, can be found. Let U and V be independent random variables such that

$$U \sim GIG(-\lambda, \delta, \gamma),$$

and

$$V \sim \Gamma(\lambda, \gamma^2/2).$$

Then if

$$(X_1, X_2) = (U^{-1}, U + V),$$

we have that $X_1 \sim GIG(\lambda, \gamma, \delta)$ and $X_2 \sim GIG(\lambda, \delta, \gamma)$. Furthermore, X_1 and X_2 have joint density

$$f_{X_1, X_2}(x_1, x_2) = \frac{(\delta\gamma)^\lambda}{2^{\lambda+1}\Gamma(\lambda)K_\lambda(\delta\gamma)} (x_1x_2 - 1)^{\lambda-1} \exp\left(-\frac{1}{2}(\delta^2x_1 + \gamma^2x_2)\right), \quad x_1, x_2 \in S_x,$$

where

$$S_x = \{(x_1, x_2) : x_1, x_2 > 0 \text{ and } x_1x_2 > 1\}.$$

In particular, for $\lambda = \frac{1}{2}$ we obtain the two-dimensional *RIG* distribution, which has density given by

$$\frac{(\delta\gamma)}{2\pi} \exp(\delta\gamma)(x_1x_2 - 1)^{-1/2} \exp\left(-\frac{1}{2}(\delta^2x_1 + \gamma^2x_2)\right), \quad x_1, x_2 \in S_x, \quad (5)$$

and Laplace transform

$$E[\exp(\theta_1X_1 + \theta_2X_2)] = \frac{\exp\left(\delta\gamma\left(1 - \sqrt{1 - \frac{2\theta_1}{\delta^2}}\sqrt{1 - \frac{2\theta_2}{\gamma^2}}\right)\right)}{\sqrt{1 - \frac{2\theta_1}{\delta^2}}\sqrt{1 - \frac{2\theta_2}{\gamma^2}}}. \quad (6)$$

Furthermore,

$$X_1 \sim RIG(\gamma, \delta), \quad \text{and} \quad X_2 \sim RIG(\delta, \gamma).$$

3 Random resistance trees

Let $T = (\mathcal{V}, \mathcal{E}, s)$ be a finite rooted tree, i.e. a connected oriented acyclic graph, with root s , set of vertices \mathcal{V} and set of edges \mathcal{E} . If $v \in \mathcal{V} \setminus \{s\}$ let $\zeta(v)$ denote the vertex preceding v according to the order on the tree. A path is a sequence $p = (v_1, \dots, v_n)$ such that $v_n = \zeta(v_{n+1})$ for all n . We define a *ray* $\pi = (s, v_1, \dots, v_n)$ as a path starting at s and such that there does not exist $v \in \mathcal{V} \setminus \pi$ for which $v_n = \zeta(v)$. Let

$$\partial T = \{\text{rays}\},$$

denote the boundary of T .

Let φ be a potential function on T , i.e. φ is a function $\varphi : \mathcal{V} \mapsto [0, \infty)$, suppose that φ is non increasing according to the natural order on T , and let

$$\psi(e) = \varphi(\zeta(v)) - \varphi(v),$$

be the drop in potential along the edge $e \in \mathcal{E}$, $e = \{\zeta(v), v\}$. We assume that φ is zero at ∂T , i.e. if $\pi = (s, v_1, \dots, v_n)$ is a ray then $\varphi(v_n) = 0$.

For $v \in \mathcal{V}$ let V_v denote the subset of the boundary which can be reached from a path starting in v and let T_v be the subtree with root v . We identify V_v and ∂T_v .

Let γ be a deterministic measure on ∂T , satisfying

$$\gamma(\partial T_v) > 0 \quad \forall v \in \mathcal{V}.$$

Furthermore, let M be a random measure on ∂T , such that

- If A and B are disjoint, then $M(A)$ and $M(B)$ are independent.
- The distribution of $M(A)$ is $IG(\gamma(A), 0)$ for any subset of ∂T .

The existence of such a random measure follows from property 2 in Section 2.

We equip the edges $e \in \mathcal{E}$, $e = \{\zeta(v), v\}$, with inverse Gaussian random variables X_e such that the X_e 's are mutually independent and

$$X_e \sim IG(\psi(e), \gamma(\partial T_v)).$$

The influence of the boundary on the resistance will be modelled by the random measure defined above, which is assumed to be independent of the X_e 's. Specifically, on the vertices in ∂T we place random resistances defined by

$$X_v = M(\partial T_v)^{-1} \sim \Gamma\left(\frac{1}{2}, \frac{1}{2}\gamma(\partial T_v)^2\right).$$

In this case ∂T_v are singletons. The tree T equipped with these random resistances we denote by \mathbf{T} .

In Barndorff-Nielsen (1994) it was shown that the total resistance of such a tree, which we denote by $R(\mathbf{T})$, is distributed as

$$R(\mathbf{T}) \sim RIG(\varphi(s), \gamma(\partial T)).$$

The total resistance is defined by the recursive formula

$$R(T) = \left(\sum_{v \in \zeta^{-1}(s)} (R_{T_v} + R_{\{s,v\}})^{-1} \right)^{-1}$$

where T_v is the complete subtree with initial vertex v .

4 Conditional distributions

In this section we will study trees with several levels of constant potential. In order to ease the notation we add the gamma random variable sitting on a terminal vertex to the edge it is at the end of; thereby the random variables on the exterior edges are reciprocal inverse Gaussian. We assume that the parameters fulfill the conditions described in the previous section, so that

$$R(\mathbf{T}) \sim RIG(\varphi(s), \gamma(\partial T)).$$

4.1 One intermediate level

We will study distributions of $X_{\mathbf{T}}$, the family of random variables in \mathbf{T} , conditional on the total resistance $R(\mathbf{T})$, under certain proportionality restrictions on the parameters. Specifically, we assume that for $e = \{\zeta(v), v\} \in \mathcal{E}_{|T'}$, where T' denotes a subtree with root s and $\mathcal{E}_{|T'}$ denotes the set of edges in T' (see Figure 2),

$$\psi(e) = \delta_1 \Delta_e \quad \text{and} \quad \gamma(\partial T_v) = \gamma \Gamma_e,$$

and for $e = \{\zeta(v), v\} \in \mathcal{E}_{|T \setminus T'}$

$$\psi(e) = \delta_2 \Delta_e \quad \text{and} \quad \gamma(\partial T_v) = \gamma \Gamma_e;$$

here the Δ_e and Γ_e are considered as known constants while δ_1 , δ_2 and γ are unknown parameters.

Suppose for a moment that $\delta_1 = \delta_2 = \delta$. In Barndorff-Nielsen & Koudou (1998) it was shown that for finite trees \mathbf{T} and for $T' = T$ the conditional distribution $X_{\mathbf{T}} | R(\mathbf{T}) = r$ is an exponential family with canonical statistic given by

$$(u', w') = \left(\sum_{e \in T} \Delta_e^2 x_e^{-1} - \Delta^2 r^{-1}, \sum_{e \in T} \Gamma_e^2 x_e - \Gamma^2 r \right),$$

where

$$\Delta = \sum_{e \in \pi} \Delta_e \quad \text{and} \quad \Gamma = \sum_{e = \{\zeta(v), v\}: v \in \partial T} \Gamma_e,$$

and canonical parameter

$$\left((\delta^2 - 1), (\gamma^2 - 1) \right).$$

Furthermore, it was shown that (given $R(\mathbf{T}) = r$) the two canonical statistics u' and w' are independent and gamma distributed. The shape parameter of u' is $|\mathcal{E}_{|T}| - |\partial T|$ and the scale parameter is $\frac{2}{\delta^2}$. $|\cdot|$ denotes the number of elements. For w' the shape parameter is $|\partial T|$ and the scale parameter is $\frac{2}{\gamma^2}$. Since the distribution of u' only depends on δ and that of w' only on γ , inference can be carried out separately. Note further that the conditional distribution of u' and w' does not depend on r , implying that u' , w' and r are independent.

Returning to the case where the potential of the tree T is described by two parameters δ_1 and δ_2 , one for the tree T' and one for $T \setminus T'$, we now add the assumption that at the boundary of T' the potential drop is the same along all rays, i.e. for some $\varphi' \in (0, \varphi(s))$

$$\sum_{e \in \pi_{|T'}} \delta_1 \Delta_e = \varphi(s) - \varphi',$$

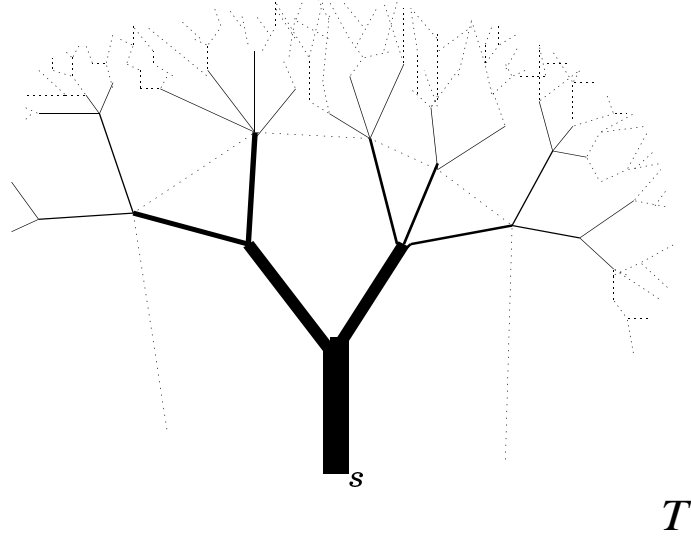


Figure 2: Example of a tree. The dotted line delimits the tree T' , where the potential fall is the same along all rays. s denotes the root of the tree.

independently of the path $\pi_{|T'}$, where $\pi_{|T'}$ is a path where all edges lie in T' . This implies that there exist constants Δ_1 and Δ_2 such that

$$\sum_{e \in \pi_{|T'}} \Delta_e = \Delta_1,$$

and

$$\sum_{e \in \pi_{|T \setminus T'}} \Delta_e = \Delta_2,$$

for all paths $\pi_{|T'}$ and $\pi_{|T \setminus T'}$. We can now write

$$\varphi(s) = (\varphi(s) - \varphi') + \varphi' = \delta_1 \Delta_1 + \delta_2 \Delta_2.$$

Also we have that

$$\begin{aligned} \sum_{e=\{\zeta(v),v\}:v \in \partial T'} \gamma \Gamma_e &= \sum_{e=\{\zeta(v),v\}:v \in \partial T} \gamma \Gamma_e = \gamma(\partial T) \\ \Rightarrow \sum_{e=\{\zeta(v),v\}:v \in \partial T'} \Gamma_e &= \sum_{e=\{\zeta(v),v\}:v \in \partial T} \Gamma_e = \Gamma, \end{aligned}$$

where $\Gamma = \gamma^{-1} \gamma(\partial T)$.

Lemma 4.1 *We have that*

$$\sum_{e \in T'} \Delta_e \Gamma_e = \Delta_1 \Gamma,$$

and

$$\sum_{e \in T \setminus T'} \Delta_e \Gamma_e = \Delta_2 \Gamma.$$

Proof of Lemma 4.1: This follows from Lemma 1 in Barndorff-Nielsen & Koudou (1998) as is seen by noting that $T \setminus T'$ can be viewed as a tree with potential fall φ' . \square

By use of the above notation we find that the probability density function of $R(\mathbf{T})$ is

$$\begin{aligned} p(r; \delta_1, \delta_2, \gamma) &= \frac{\gamma \Gamma}{\sqrt{2\pi}} \exp(\delta_1 \gamma \Delta_1 \Gamma) \exp(\delta_2 \gamma \Delta_2 \Gamma) r^{-1/2} \\ &\times \exp\left(-\frac{1}{2} \delta_1^2 \Delta_1^2 r^{-1}\right) \exp\left(-\frac{1}{2} \delta_2^2 \Delta_2^2 r^{-1}\right) \exp\left(-\delta_1 \delta_2 \Delta_1 \Delta_2 r^{-1}\right) \\ &\times \exp\left(-\frac{1}{2} \gamma^2 \Gamma^2 r\right). \end{aligned}$$

Further by Lemma 4.1, the probability density function for $X_{\mathbf{T}'}, X_{\mathbf{T} \setminus \mathbf{T}'}$ is given by

$$\begin{aligned} p(x_{\mathbf{T}'}, x_{\mathbf{T} \setminus \mathbf{T}'}; \delta_1, \delta_2, \gamma) &= \\ &\left(\frac{\delta_1}{\sqrt{2\pi}}\right)^{|\mathcal{E}_{|T'}|} \left(\frac{\delta_2}{\sqrt{2\pi}}\right)^{|\mathcal{E}_{|T \setminus T'}| - |\partial T|} \left(\frac{\gamma}{\sqrt{2\pi}}\right)^{|\partial T|} \\ &\times \exp\left(\delta_1 \gamma \sum_{e \in T'} \Delta_e \Gamma_e\right) \exp\left(\delta_2 \gamma \sum_{e \in T \setminus T'} \Delta_e \Gamma_e\right) \\ &\times \left(\prod_{e \in T'} \Delta_e x_e^{-3/2}\right) \left(\prod_{e=\{\zeta(v), v\} \in T \setminus T': v \notin \partial T} \Delta_e x_e^{-3/2}\right) \\ &\times \left(\prod_{e=\{\zeta(v), v\} \in T \setminus T': v \in \partial T} \Gamma_e x_e^{-1/2}\right) \exp\left(-\frac{1}{2} \left(\delta_1^2 \sum_{e \in T'} \Delta_e^2 x_e^{-1}\right)\right) \\ &\times \exp\left(-\frac{1}{2} \left(\delta_2^2 \sum_{e \in T \setminus T'} \Delta_e^2 x_e^{-1}\right)\right) \exp\left(-\frac{1}{2} \left(\gamma^2 \sum_{e \in T} \Gamma_e^2 x_e\right)\right). \end{aligned} \quad (7)$$

Theorem 4.1 *By letting*

$$u_1 = \sum_{e \in T'} \Delta_e^2 x_e^{-1}, \quad u_2 = \sum_{e \in T \setminus T'} \Delta_e^2 x_e^{-1}, \quad w = \sum_{e \in T} \Gamma_e^2 x_e,$$

and

$$u'_1 = u_1 - \Delta_1^2 r^{-1}, \quad u'_2 = u_2 - \Delta_2^2 r^{-1} \quad \text{and} \quad w' = w - \Gamma^2 r.$$

we have that

1. $\{p(x_{\mathbf{T}'}, x_{\mathbf{T} \setminus \mathbf{T}'}; \delta_1, \delta_2, \gamma); \delta_1 > 0, \delta_2 > 0, \gamma > 0\}$ is an exponential family with canonical statistic (u_1, u_2, w) and canonical parameter given by $-\frac{1}{2}(\delta_1^2, \delta_2^2, \gamma^2)$.
2. $w'|r$ is independent of $(u'_1, u'_2)|r$, and $w'|r$ is gamma distributed with shape parameter $|\partial T| - 1$ and scale parameter $\frac{2}{\gamma^2}$. Furthermore, conditional on $R(\mathbf{T})$, the distribution of (u'_1, u'_2) depends only on (δ_1, δ_2) , hence, the inference for (δ_1, δ_2) depends only on (u'_1, u'_2) and the inference for γ depends only on w' .

Proof of Theorem 4.1:

1. Follows directly from formula (7).

2. Now let us look at the family of conditional distributions

$\{p(x_{\mathbf{T}'}, x_{\mathbf{T} \setminus \mathbf{T}'}; \delta_1, \delta_2, \gamma | R(\mathbf{T}) = r); \delta_1 > 0, \delta_2 > 0, \gamma > 0\}$. We find

$$\begin{aligned} \frac{p(x_{\mathbf{T}'}, x_{\mathbf{T} \setminus \mathbf{T}'}; \delta_1, \delta_2, \gamma | R(\mathbf{T}) = r)}{p(x_{\mathbf{T}'}, x_{\mathbf{T} \setminus \mathbf{T}'}; 1, 1, 1 | R(\mathbf{T}) = r)} &= \frac{p(x_{\mathbf{T}'}, x_{\mathbf{T} \setminus \mathbf{T}'}; \delta_1, \delta_2, \gamma)}{p(x_{\mathbf{T}'}, x_{\mathbf{T} \setminus \mathbf{T}'}; 1, 1, 1)} \\ &= \frac{p(r; \delta_1, \delta_2, \gamma)}{p(r; 1, 1, 1)} \\ &= (\delta_1)^{|\mathcal{E}_{|T'}|} (\delta_2)^{|\mathcal{E}_{|T \setminus T'}| - |\partial T|} (\gamma)^{|\partial T| - 1} \exp\left((\delta_1 \delta_2 - 1) \Delta_1 \Delta_2 r^{-1}\right) \\ &\times \exp\left(-\frac{1}{2} \left((\delta_1^2 - 1) u'_1 + (\delta_2^2 - 1) u'_2 \right)\right) \exp\left(-\frac{1}{2} (\gamma^2 - 1) w'\right). \end{aligned}$$

Hence, by letting $A = |\mathcal{E}_{|T'}|$, $B = |\mathcal{E}_{|T \setminus T'}| - |\partial T|$ and $C = |\partial T| - 1$ we have that the Laplace transform of $(u'_1, u'_2, w')|r$ is given by

$$\begin{aligned} E[\exp(\theta_1 u'_1 + \theta_2 u'_2 + \theta_3 w') | r] &= \\ &\left(1 - \frac{2\theta_1}{\delta_1^2}\right)^{-A/2} \left(1 - \frac{2\theta_2}{\delta_2^2}\right)^{-B/2} \left(1 - \frac{2\theta_3}{\gamma^2}\right)^{-C/2} \\ &\times \exp\left(\Delta_1 \Delta_2 r^{-1} \delta_1 \delta_2 \left(1 - \sqrt{\left(1 - \frac{2\theta_1}{\delta_1^2}\right) \left(1 - \frac{2\theta_2}{\delta_2^2}\right)}\right)\right). \end{aligned}$$

The Laplace transform is seen to be a product of

$$E[\exp(\theta_3 w') | r] = \left(1 - \frac{2\theta_3}{\gamma^2}\right)^{-C/2},$$

and

$$E[\exp(\theta_1 u'_1 + \theta_2 u'_2) | r] =$$

$$\begin{aligned} & \left(1 - \frac{2\theta_1}{\delta_1^2}\right)^{-A/2} \left(1 - \frac{2\theta_2}{\delta_2^2}\right)^{-B/2} \\ & \times \exp\left(\Delta_1\Delta_2r^{-1}\delta_1\delta_2\left(1 - \sqrt{\left(1 - \frac{2\theta_1}{\delta_1^2}\right)\left(1 - \frac{2\theta_2}{\delta_2^2}\right)}\right)\right). \end{aligned} \quad (8)$$

Consequently, $w'|r$ is independent of $(u'_1, u'_2)|r$, and $w'|r$ is gamma distributed with shape parameter C and scale parameter $\frac{2}{\gamma^2}$. Furthermore, the above formulae imply that, conditional on $R(\mathbf{T})$, the inference for (δ_1, δ_2) only depends on (u'_1, u'_2) and the inference for γ only depends on w' . \square

Remark

If $\delta_1 = \delta_2$ we get the same result as Barndorff-Nielsen & Koudou (1998). To see this note that

$$u'_1 + u'_2 = u' + 2\Delta_1\Delta_2r^{-1},$$

and that

$$\Delta_1\Delta_2r^{-1}\delta_1^2\left(1 - \sqrt{\left(1 - \frac{2\theta_1}{\delta_1^2}\right)\left(1 - \frac{2\theta_1}{\delta_1^2}\right)}\right) = 2\Delta_1\Delta_2r^{-1}\theta_1.$$

Remark

By (8)

$$E[\exp(\theta_1 u'_1) | r] = \left(1 - \frac{2\theta_1}{\delta_1^2}\right)^{-A/2} \exp\left(\Delta_1\Delta_2r^{-1}\delta_1\delta_2\left(1 - \sqrt{1 - \frac{2\theta_1}{\delta_1^2}}\right)\right), \quad (9)$$

and

$$E[\exp(\theta_2 u'_2) | r] = \left(1 - \frac{2\theta_2}{\delta_2^2}\right)^{-B/2} \exp\left(\Delta_1\Delta_2r^{-1}\delta_1\delta_2\left(1 - \sqrt{1 - \frac{2\theta_2}{\delta_2^2}}\right)\right). \quad (10)$$

and hence we have that

$$\begin{aligned} u'_1|r & \sim \Gamma\left(\frac{A}{2}, \frac{\delta_1^2}{2}\right) * IG(\Delta_1\Delta_2r^{-1}\delta_2, \delta_1) \\ & = \Gamma\left(\frac{A-1}{2}, \frac{\delta_1^2}{2}\right) * RIG(\Delta_1\Delta_2r^{-1}\delta_2, \delta_1), \end{aligned} \quad (11)$$

$$\begin{aligned} u'_2|r & \sim \Gamma\left(\frac{B}{2}, \frac{\delta_2^2}{2}\right) * IG(\Delta_1\Delta_2r^{-1}\delta_1, \delta_2) \\ & = \Gamma\left(\frac{B-1}{2}, \frac{\delta_2^2}{2}\right) * RIG(\Delta_1\Delta_2r^{-1}\delta_1, \delta_2). \end{aligned} \quad (12)$$

In the light of this and (8) it is natural to ask whether

$$\begin{aligned} & \left(1 - \frac{2\theta_1}{\delta_1^2}\right)^{-1/2} \left(1 - \frac{2\theta_2}{\delta_2^2}\right)^{-1/2} \\ & \times \exp\left(\Delta_1\Delta_2r^{-1}\delta_1\delta_2 \left(1 - \sqrt{\left(1 - \frac{2\theta_1}{\delta_1^2}\right)\left(1 - \frac{2\theta_2}{\delta_2^2}\right)}\right)\right) \end{aligned} \quad (13)$$

is the Laplace transform of a two-dimensional density function. If so, (13) determines a two-dimensional distribution whose marginals are the reciprocal inverse Gaussian laws $RIG(\Delta_1\Delta_2r^{-1}\delta_2, \delta_1)$ and $RIG(\Delta_1\Delta_2r^{-1}\delta_1, \delta_2)$, cf. (11) and (12). The problem of creating two-dimensional densities with reciprocal inverse Gaussian or inverse Gaussian marginals has been given some attention in the literature, see e.g. Barndorff-Nielsen et al. (1992). From the results of that paper, restated in Section 2 above, it follows that, in fact, the quantity (13) is the Laplace transform of a probability density function given by

$$\frac{\delta_1\delta_2 \exp(\Delta_1\Delta_2r^{-1}\delta_1\delta_2)}{2\pi} (x_1x_2 - \Delta_1\Delta_2r^{-1})^{-1/2} \exp\left(-\frac{1}{2}(\delta_1^2x_1 + \delta_2^2x_2)\right),$$

where $x_1, x_2 \in S_x$ and $S_x = \{(x_1, x_2) : x_1, x_2 > 0 \wedge x_1x_2 > \Delta_1\Delta_2r^{-1}\}$, cf. formula (5). This type of density function comes about the same way as (5) in Section 2, namely by letting

$$(X_1, X_2) = \left(\left(\Delta_1\Delta_2r^{-1}\right)^2 U^{-1}, U + V\right),$$

where

$$U \sim IG(\Delta_1\Delta_2r^{-1}\delta_1, \delta_2) \quad \text{and} \quad V \sim \Gamma\left(\frac{1}{2}, \frac{\delta_2^2}{2}\right).$$

While the two-dimensional *RIG* distribution (5) was introduced in Barndorff-Nielsen et al. (1992) as a purely mathematical construct, in the present biological motivated context, it arises naturally through conditioning on $R(\mathbf{T})$.

4.2 Several levels

Now, let us turn to a situation where we are interested in several intermediate specific potential levels instead of only one. We restrict ourselves to two levels as this is enough to indicate the general structure. Let $s \subseteq T' \subseteq T'' \subseteq T$ such that at the boundaries of these subtrees the potential is constant and $0 < \varphi'' < \varphi' < \varphi(s)$ where φ' and φ'' are the potentials at the boundary of T' and T'' respectively.

Then we find

$$\begin{aligned}
& \frac{p\left(x_{\mathbf{T}'}, x_{\mathbf{T}'' \setminus \mathbf{T}'}, x_{\mathbf{T} \setminus \mathbf{T}''}; \delta_1, \delta_2, \delta_3, \gamma \mid R(\mathbf{T}) = r\right)}{p\left(x_{\mathbf{T}'}, x_{\mathbf{T} \setminus \mathbf{T}'}; 1, 1, 1, 1 \mid R(\mathbf{T}) = r\right)} = \\
& = (\delta_1)^{|\mathcal{E}_{|\mathbf{T}'|}|} (\delta_2)^{|\mathcal{E}_{|\mathbf{T}'' \setminus \mathbf{T}'|}|} (\delta_3)^{|\mathcal{E}_{|\mathbf{T} \setminus \mathbf{T}''|} - |\partial \mathbf{T}|} (\gamma)^{|\partial \mathbf{T}| - 1} \\
& \times \exp\left((\delta_1 \delta_2 - 1) \Delta_1 \Delta_2 r^{-1}\right) \exp\left((\delta_1 \delta_3 - 1) \Delta_1 \Delta_3 r^{-1}\right) \exp\left((\delta_2 \delta_3 - 1) \Delta_2 \Delta_3 r^{-1}\right) \\
& \times \exp\left(-\frac{1}{2} \left((\delta_1^2 - 1) u'_1 + (\delta_2^2 - 1) u'_2 + (\delta_3^2 - 1) u'_3 \right)\right) \exp\left(-\frac{1}{2} (\gamma^2 - 1) w'\right),
\end{aligned}$$

where

$$\begin{aligned}
u'_1 &= \sum_{e \in \mathbf{T}'} \Delta_e^2 x_e^{-1} - \Delta_1^2 r^{-1} & u'_2 &= \sum_{e \in \mathbf{T}'' \setminus \mathbf{T}'} \Delta_e^2 x_e^{-1} - \Delta_2^2 r^{-1} \\
u'_3 &= \sum_{e \in \mathbf{T} \setminus \mathbf{T}''} \Delta_e^2 x_e^{-1} - \Delta_3^2 r^{-1} & w' &= \sum_{e \in \mathbf{T}} \Gamma_e^2 x_e - \Gamma^2 r,
\end{aligned}$$

and where

$$\sum_{e \in \pi_{|\mathbf{T}'|}} \Delta_e = \Delta_1, \quad \sum_{e \in \pi_{|\mathbf{T}'' \setminus \mathbf{T}'|}} \Delta_e = \Delta_2 \quad \text{and} \quad \sum_{e \in \pi_{|\mathbf{T} \setminus \mathbf{T}''|}} \Delta_e = \Delta_3,$$

for all paths $\pi_{|\mathbf{T}'|}$, $\pi_{|\mathbf{T}'' \setminus \mathbf{T}'|}$ and $\pi_{|\mathbf{T} \setminus \mathbf{T}''|}$. Furthermore,

$$\begin{aligned}
& \sum_{e=\{\zeta(v), v\}: v \in \partial \mathbf{T}'} \gamma \Gamma_e = \sum_{e=\{\zeta(v), v\}: v \in \partial \mathbf{T}''} \gamma \Gamma_e = \sum_{e=\{\zeta(v), v\}: v \in \partial \mathbf{T}} \gamma \Gamma_e = \gamma(\partial \mathbf{T}) \\
\Rightarrow & \sum_{e=\{\zeta(v), v\}: v \in \partial \mathbf{T}'} \Gamma_e = \sum_{e=\{\zeta(v), v\}: v \in \partial \mathbf{T}''} \Gamma_e = \sum_{e=\{\zeta(v), v\}: v \in \partial \mathbf{T}} \Gamma_e = \Gamma,
\end{aligned}$$

where $\Gamma = \gamma^{-1} \gamma(\partial \mathbf{T})$. Thereby we get that

$$\begin{aligned}
& E[\exp(\theta_1 u'_1 + \theta_2 u'_2 + \theta_3 u'_3 + \theta_4 w')] = \\
& \left(1 - \frac{2\theta_1}{\delta_1^2}\right)^{-A/2} \left(1 - \frac{2\theta_2}{\delta_2^2}\right)^{-B/2} \left(1 - \frac{2\theta_3}{\delta_3^2}\right)^{-C/2} \left(1 - \frac{2\theta_4}{\gamma^2}\right)^{-D/2} \\
& \times \exp\left(\Delta_1 \Delta_2 r^{-1} \delta_1 \delta_2 \left(1 - \sqrt{\left(1 - \frac{2\theta_1}{\delta_1^2}\right) \left(1 - \frac{2\theta_2}{\delta_2^2}\right)}\right)\right) \\
& \times \exp\left(\Delta_1 \Delta_3 r^{-1} \delta_1 \delta_3 \left(1 - \sqrt{\left(1 - \frac{2\theta_1}{\delta_1^2}\right) \left(1 - \frac{2\theta_3}{\delta_3^2}\right)}\right)\right) \\
& \times \exp\left(\Delta_2 \Delta_3 r^{-1} \delta_2 \delta_3 \left(1 - \sqrt{\left(1 - \frac{2\theta_2}{\delta_2^2}\right) \left(1 - \frac{2\theta_3}{\delta_3^2}\right)}\right)\right),
\end{aligned}$$

where

$$A = |\mathcal{E}_{|\mathbf{T}'|}|, \quad B = |\mathcal{E}_{|\mathbf{T}'' \setminus \mathbf{T}'|}| - |\partial \mathbf{T}|, \quad C = |\mathcal{E}_{|\mathbf{T} \setminus \mathbf{T}''|}| - |\partial \mathbf{T}| \quad \text{and} \quad D = |\partial \mathbf{T}| - 1.$$

This implies that $w'|r$ is independent of $(u'_1, u'_2, u'_3)|r$ and, like in the case with only one level, $w'|r$ is gamma distributed with shape parameter D and scale parameter $\frac{2}{\gamma^2}$. It should also be noted that the distribution of $(u'_1, u'_2, u'_3)|r$ is a convolution of three gamma distributions and three two-dimensional reciprocal inverse Gaussian distributions, which are all independent. In fact, the convolution of the three two-dimensional reciprocal inverse Gaussian distributions gives us a new type of three-dimensional reciprocal inverse Gaussian distribution which has reciprocal inverse Gaussian distributed one-dimensional marginals, as can be seen from below, and two-dimensional marginals each of which is a convolution of a two-dimensional reciprocal inverse Gaussian distribution and two reciprocal inverse Gaussian distributions, which are independent. Further, it is seen that the distribution of $u'_1|r$ depends only on δ_2 and δ_3 through $\varphi(s)$ since

$$\begin{aligned} E[\exp(\theta_1 u'_1)] &= \\ &= \left(1 - \frac{2\theta_1}{\delta_1^2}\right)^{-A/2} \exp\left(\Delta_1 r^{-1} \delta_1 (\Delta_2 \delta_2 + \Delta_3 \delta_3) \left(1 - \sqrt{\left(1 - \frac{2\theta_1}{\delta_1^2}\right)}\right)\right) \\ &= \left(1 - \frac{2\theta_1}{\delta_1^2}\right)^{-A/2} \exp\left(\Delta_1 r^{-1} \delta_1 (\varphi(s) - \Delta_1 \delta_1) \left(1 - \sqrt{\left(1 - \frac{2\theta_1}{\delta_1^2}\right)}\right)\right), \end{aligned}$$

and we also see that $u'_1|r$ is a convolution of a gamma distributed random variable with shape parameter A and scale parameter $\frac{2}{\delta_1^2}$ and an inverse Gaussian distributed random variable with parameters $\Delta_1 r^{-1}(\varphi(s) - \Delta_1 \delta_1)$ and δ_1 .

The above-mentioned results raise the question of what physical interpretation may be given of the statistics u', w', u'_1, u'_2 etc.. We have not been able to resolve this.

4.3 Extension

It was assumed above that the potential function was constant at one or more levels (apart from the end vertices where φ is always 0 by assumption). However, consider the tree cut as indicated by Figure 3 and extend the potential function φ to a non-increasing function along all edges, such that it is constant at the points where the dashed curve cuts the tree. Theorem 4.1 may then be extended to the present setting, in view of the convolution property 2.

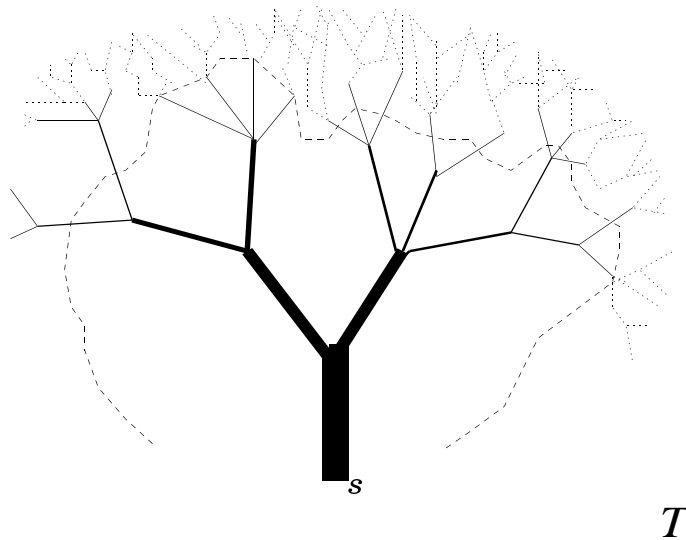


Figure 3: Example of a tree. The dashed line delimits the tree T' , where the potential fall is the same along all rays. s denotes the root of the tree.

Acknowledgement

Most of the work was done while the second author was at the University of Aarhus. We are grateful to Gerard Letac for helpful discussions.

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